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VOLUME XLVII NUMBER 1

BOTANICAL GAZETTE

JANUARY 1909

ON TRIPLE HYBRIDS

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Twin hybrids are produced when the pollen of *Oenothera Lamarckiana* or of one of its derivatives is crossed with the European subspecies of *O. biennis* or of *O. muricata*. These twins appear in about equal numbers and are constant in succeeding generations. One of them, *O. laeta*, is broad and smooth leaved; the other, *O. velutina*, is more hairy and has furrow-shaped leaves.[1]

Triple hybrids may be produced by combining this phenomenon with the hereditary qualities of *O. lata* and *O. scintillans*. Both of them originated in my garden from *O. Lamarckiana*. *O. lata* is female, its anthers are barren. *O. scintillans* is an inconstant species which repeats its type only in one-third or two-thirds of its offspring. Both of them, when pollinated by *O. Lamarckiana*, give a mixed progeny, only part of which is like the mother.[2]

In order to get triplets, therefore, we have to cross *O. lata* or *O. scintillans* with some species which will split them into *laeta* and *velutina* (as it would do *O. Lamarckiana* itself or some others of its mutant species), and which, moreover, does not prevent them from repeating their own type in their progeny. The triplets will then be *O. laeta*, *O. velutina*, and *O. lata*. The first two will drop the special character of the mutant-parent (BOT. GAZ. *l. c.* 403), but all three will be intermediate hybrids between *O. Lamarckiana* or *O. lata* and the species used as the other parent.

I found that *O. strigosa* Rydberg, *O. Hookeri* T. and G., and the common American subspecies of *O. biennis* L. comply with these

[1] BOT. GAZETTE **44**:401–407. 1907.

[2] *Die Mutations-Theorie.* Vols. I and II.

requirements. The experiments to be described in this article are limited to the effects of their pollen on *O. lata* and *O. scintillans*.

O. strigosa Rydb. has very small flowers, of the size of those of *O. muricata*, but in less dense spikes. They open their anthers two or more days before unfolding the corolla, and the pollen comes in contact with the whole outer surface of the stigma and causes fertilization. The leaves are bluish green and furrow-shaped, and the tip is bent sideways. The tops of young shoots, when seen from above, therefore, present the aspect of a wheel with spokes all curved to the left or to the right. This striking feature is repeated, though somewhat reduced, in all of its hybrids and causes them to be easily recognized. I collected seed in the Yellowstone Park in 1904. Another lot was kindly sent to me by Mr. T. D. A. COCKERELL from Boulder, Colorado. Of both strains I have since cultivated two generations.

In crossing *O. strigosa* with *O. Lamarckiana*, twins arise which combine the characters of *laeta* and *velutina* with those of *strigosa*. They differ more widely from one another than do the twins of any other cross I have studied up to this time. The *velutina* is almost like the *velutina* of *O. muricata* × *Lamarckiana*, but has the bluish tinge, the more pointed leaves with bent tips, and the wheel-shaped tops of the young shoots described above for *O. strigosa*. The *laeta* from the *strigosa* cross is a very stout plant with very broad leaves (6^{cm}), blunt at the apex and indented at the base, with smooth surface, and bright green. The flower buds are more narrowly conical than those of *velutina*, the flowers open more widely, the fruits are conical with four sharp and protruding teeth, whereas those of *velutina* are blunt and short. By this mark and by the somewhat narrowed neck of the fruits of *velutina*, the two forms are most easily distinguished when flowering is over. The *laeta* is usually poor, but the *velutina* is rich in pollen.

In contrast to the species previously dealt with, *O. strigosa* produces twins from *O. Lamarckiana* when used as male parent as well as when used as female parent. In these reciprocal crosses both of the twins are identical.

The twins produced by *O. strigosa* from *O. scintillans* and from *O. lata* comply with the description given. They cannot be distin-

guished from them externally, even when cultivated in large and pure lots.

O. Hookeri T. and G. is a Californian species and is also found in Texas.[3] I collected seeds in the vicinity of Berkeley, California, and another lot was sent to me from Riverside by Mr. FRED M. REED. It is a striking species, even more beautiful than *O. Lamarckiana*. The flowers are of the same size, protruding their pistils high above the anthers; but the petals are more deeply emarginate at the tip, nearly obcordate, and a paler yellow. The plant is hairy and reddish, and the leaves (especially those of the rosette) are long and narrow.

With *Lamarckiana* it produces twins identical in both reciprocal crosses and both of them as large-flowered as the parent species. The *laeta* is bright green, with smooth leaves and slender flower buds. The *velutina* is hairy and reddish, with furrow-shaped leaves and thick buds. It flowers more profusely and resembles *O. Hookeri* almost exactly, but is stouter, with dense and richly flowered spikes.

The twins derived by *O. Hookeri* from *O. lata* cannot be distinguished externally from those derived from *O. Lamarckiana*.

The American subspecies of *O. biennis* used for my experiments was collected by me in 1904 at Chicago, near Jackson Park. It seems to be the same form as that which is most common in the eastern states. Other subspecies I have collected in Pennsylvania, Kansas, Missouri, and elsewhere. All of them are quite different from the European form, which is the one used in my *Mutations-Theorie* and in my article on twin hybrids (BOT. GAZETTE *l. c.*). A systematic treatment of these numerous forms is still wanting, and therefore I will provisionally designate my strain by the name of its source and call it *Chicago*. Its most curious quality is that of producing twins when combined as a male parent with *O. Lamarckiana* and not when crossed with the pollen of this species. In this respect it is exactly opposite to the European *O. biennis*, and therefore very useful.

The *O. biennis* from Chicago is a taller plant, more richly branched, and darker green than the European form. Its flowers are much smaller, sometimes reaching the size of those of *O. muricata*, but

[3] *Oen. Hookeri* T. and G.=*Onagra Hookeri* Small=*O. biennis hirsutissima* Gray, Bot. Calif. See H. M. HALL, A botanical survey of San Jacinto Mountain. Univ. Calif. Publ. Bot. 1:98. 1902.

deeper yellow. The stigma is surrounded by the anthers which open early in the bud. The *velutina* and *laeta* which it produces from *Lamarckiana* can hardly be distinguished from those produced by the European *O. biennis*, although the leaves are narrower and darker green. I cultivated this strain during three succeeding generations.

O. scintillans and *O. lata* are the mutant species described in my *Mutations-Theorie*. The *scintillans* used originated from *Lamarckiana* seed of 1889 which was sown in 1895. In 1906 I had the fourth generation from continued pure self-fertilizations and used it for my cross. From this same strain the *lata* used in the experiments of this article arose as a mutant in 1901. It was artificially fertilized. My crosses were made with specimens of the second and third generation of its progeny.

I will now describe the crosses from which the triplets resulted.

Oenothera scintillans × *strigosa*.—This cross was made in July, 1907, between two biennial specimens. It yielded a small lot of seed which was sown the next spring. From it arose 36 *laeta*, 21 *velutina*, 15 *scintillans*, and one *lata*, altogether 73 plants, most of which flowered during the summer. The *laeta* and *velutina* agreed with the description given above; the *lata* was a mutant. The *scintillans* were intermediate hybrids, which had the habit and leaves of the mother parent, or nearly so, but small flowers with the anthers surrounding and touching the stigma like the father. I fertilized all three forms with their own pollen and intend to sow the seed next year.

Oenothera lata × *strigosa*.—This cross was effected in 1905, both parents being annual specimens. I used different plants of *lata* and sowed the seed of one cross in 1906, of another cross in 1907, and a third lot in 1908. I got the following results:

Year	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1906	41	36	59	5
1907	47	49	40	11
1908	270	27	34	38
Total	358	40	33	27

The *laeta* and *velutina* were the same as those from the cross with *Lamarckiana*. I sowed self-fertilized seed from plants of 1906 in 1907; the mothers were *velutina* and gave 113 children, most of which

flowered. All of them were *velutina*. In 1907 I self-pollinated some *laeta* and some *velutina* and got 80 and 45 seedlings respectively. The first were all *laeta*, the second lot was uniformly *velutina*. Of each lot 25 specimens were preserved after the sorting period and observed during the time of flowering and ripening of their fruits.

The *lata* were intermediate between *O. lata* and *O. strigosa*. In 1908 I cultivated one half of them in the open and the other under an open glass-covering, both of them with cultures of ordinary *lata* under the same conditions for comparison. The *lata* from the *strigosa* cross had narrower leaves but with the rounded tips; the bracts were broad but less bent downward. The flowers were much smaller than those of the mother, but somewhat larger than those of the father. Their shape resembled that of *O. strigosa*, but the stigma showed, although in a lessened degree, the peculiar hand-shaped form of the ordinary *O. lata*. The anthers touched the stigma, but only with their lower halves. The flower buds were broad, and the tube was relatively short. In all these points and in the other characters the *lata* hybrids were strikingly intermediate between the two parents. Even the bent tips of the young leaves were to be seen, and at once revealed the father. But the most interesting feature was that of the pollen. *O. lata* is purely female, while *O. strigosa* has the ordinary supply of pollen. The hybrids showed some pollen and a relatively small number of fertile grains. These were, during ordinary weather, insufficient for fertilization, even if the pollen of many flowers was brought upon one stigma. But there were individual fluctuations, and so I succeeded in getting self-fertilized fruits on at least one specimen.

Oenothera lata × *O. biennis Chicago*.—This cross was made in 1905, both parents being annual. Two specimens of *O. lata* were used. I sowed their seed in different lots in the three succeeding years and had the following results:

Year	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1906	33	27	70	3
1907	78	34	29	37
1908	167	36	28	35
Total	278	35	34	31

The *laeta* and the *velutina* were of the description already given. I sowed the self-fertilized seed of 1906 in 1907 and 1908 and had four lots of the second generation. The lots of the first included 69 and 139 individuals, all of which were *laeta;* the sowings of the other strain extended over 38 and 158 samples, all of which were *velutina.* Both of the twins thus complied with the rule of constancy in the second generation. From the lots of 1907 I cultivated in 1908 a third generation comprising 70 children of *laeta* and 90 of *velutina;* both lots were once more uniform and similar to their parents.

The *lata* individuals of this cross were almost similar to those of *O. lata* itself. However, they had the smaller flowers of *O. biennis,* with the self-fertilizing position of the stigma, and the long lobes of the father. Their flower buds were intermediate between those of the two parents. In 1906 and 1907 the anthers seemed wholly barren; but in 1908, during the very warm last days of July, they yielded some pollen, which was used partly for self-fertilization, partly for crosses.

O. lata × *Hookeri.*—This cross is the most interesting of all the crosses with *O. lata,* since its *lata* hybrids are almost as rich in pollen as any other evening primrose. This enabled me to study the second generation of the *lata,* which, in contrast to that of the *laeta* and the *velutina,* repeats the splitting. The yield of the pollen was small in the unfavorable summer of 1907, but large during the hot days of July and August, 1908.

I have made this cross twice, in 1905 and 1907; the parents were annual specimens. I had the following results in the first generation:

Year	Seed of	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1907	1905	51	53	39	8
1908	1905	229	45	47	8
1908	1907	72	49	28	22
Total		352	47	42	11

Here also the *laeta* and *velutina* were the same as those from the cross with *Lamarckiana.* I sowed some self-fertilized seed of the *velutina* of 1906, partly in 1907 and partly in 1908, and cultivated

from each lot 60 specimens, all of which repeated the *velutina* characters.

The *lata* specimens also were cultivated from seed of 1906 in both succeeding years. Their flowers were as large as those of both parents and intermediate in the tinge of the yellow, the *Hookeri* being paler yellow than the *Lamarckiana* and its *lata*. The anthers did not reach the stigma, which was often hand-shaped. The spike was much denser than that of *Hookeri* but thinner than that of the mother. Stem, veins, and calyx were reddish; and leaves were narrower than in *O. lata*. In all these and in other characters the plants were strikingly *lata*, but with the addition of the differentiating marks of the *Hookeri*.

The self-fertilized seed of the *lata* plants of the first generation gave a mixed progeny, consisting of *velutina* and *lata*, both resembling the types of the first year. No *laeta* specimens were produced. The numbers were the following:

Year	Number of seedlings	Percentage *velutina*	Percentage *lata*
1907.....	53	85	15
1908.....	134	81	19
Total.....	187	82	18

From the experiments described the following table may be compiled:

TRIPLE HYBRIDS AND THEIR SUCCEEDING GENERATIONS

Mother	Father	First generation Percentage	Second generation	Third generation
O. scintillans	×O. strigosa.....	49 laeta 29 velutina 21 scintillans		
O. lata	×O. strigosa.....	40 laeta 33 velutina 27 lata	80 laeta 158 velutina	
O. lata	×O. bien. Chicago.....	35 laeta 34 velutina 31 lata	208 laeta 196 velutina	70 laeta 90 velutina
O. lata	×O. Hookeri.....	47 laeta 42 velutina 11 lata	120 velutina 82 per cent. velutina 18 per cent. lata	

QUADRUPLE HYBRIDS.—The discovery of twin and triple hybrids naturally suggests the idea of the possibility of a hybrid quartette. As a matter of fact the experiments did the same. In the case of *O. lata* × *O. biennis* from Chicago a fourth type appeared in one specimen, and in that of *O. lata* × *O. Hookeri* in two specimens. These three plants belonged evidently to the *lata* type, but combined with this the smooth, broad, and bright-green leaves of the *laeta*, whereas all the other *latas* of these crosses had gray and furrow-shaped leaves like the *velutina*. The *lata-laeta* of the first cross was sufficiently fertile, but of two of the *Hookeri* cross one had barren anthers and the other only some spare pollen in comparison with the rich supply of pollen in the other *lata* plants of this cross. In this respect, therefore, they also showed the character of the *laeta* type.

It would seem probable that the *lata-laeta* should be produced in the same number as the other *lata*, or *lata-velutina* as we could now call it. But then the *laeta* itself often appears in too small numbers. The cause of this phenomenon has still to be investigated.

Summary

1. Triple hybrids are produced in crosses of *Oenothera scintillans* and *O. lata* by such species as produce twins from *O. Lamarckiana*.

2. The species investigated are *O. strigosa* Rydb., *O. Hookeri* T. and G., and one of the American subspecies of *O. biennis*.

3. Of the triple hybrids, two are the same as the twins from the corresponding *Lamarckiana* crosses and bear the characters of *O. laeta* and *O. velutina* combined with those of the other parent.

4. The third type resembles the mother (*O. lata* or *O. scintillans*), but in its special marks is also intermediate between its parents.

5. The *laeta* and *velutina* are constant and uniform in their succeeding generations, so far as experience goes. In this respect they follow the rule for the twin hybrids of *O. Lamarckiana*.

6. The *lata*, however, in the only case tried, repeated the splitting after self-fertilization, producing, however, only *lata* and *velutina*.

7. It seems probable that the whole progeny of the crosses named should split up into two equal parts, *laeta* and *velutina*, and that each of them should produce a certain percentage of *lata*. In this way quadruple hybrids would arise.

BOTANIC GARDEN
AMSTERDAM

PERIODICITY IN SPIROGYRA

W. F. COPELAND

The object in beginning these studies with Spirogyra was to get notes on the rearing of species and to see how far they could be changed by conditions. With this end in view 100 aquaria were started and soon contained puzzling results. To interpret these and to get on with the experiments, it soon seemed desirable, if not necessary, to know how Spirogyra lives under natural environment. For this reason the major part of my time was given to a consideration of this plant out of doors. An attempt has been made to repeat all observations and experiments under as great a variety of conditions as possible in an ordinary biological laboratory. When field-work was not practicable or necessary, laboratory work was resumed. In this way scores of experiments have been in progress from the beginning.

After this work had continued for some months, considerations were given to conditions appearing with some regularity whether Spirogyra was being studied under natural or under artificial environment. As a possible constant condition, it was finally decided to give special attention to the subject of periodicity. In this paper only those experiments will be mentioned which seem to have some bearing on this subject. Although laboratory studies are of minor importance in the subject of periodicity, in the present discussion they will appear first.

I take this opportunity to express my obligation to those who have in any way aided me in the present study. It is a pleasure to thank Dr. C. F. HODGE, who suggested the problem, for his help and criticism; HELEN REINHERR COPELAND for help in identification of species and preparation of material for microphotographs; O. W. MILLS, Millbury, Mass., for collecting much valuable material in that locality; and Dr. O. P. DELLINGER, Worcester, Mass., for helpful suggestions and criticisms. The following persons have sent me conjugating specimens from more distant localities: W. D. HOYT and I. F. LEWIS of Johns Hopkins University; B. A. PLACE, Iowa

Wesleyan University; S. G. WINTER, Illinois Wesleyan University; and W. A. MATHENY, Sardis, Ohio.

Review of literature

In 1803 VAUCHER (**6**) tells of his attempt to work out the life-history of the Conjugatae. For this purpose the genus Spirogyra was used and especially the species which MÜLLER had previously described as *Conferva jugalis*. VAUCHER's observations were made in the spring and it was found that this species would fruit and disappear as early as February 15 and as late as March 20. The zygospores which he had collected germinated July 15, and all seemed to germinate on the same day.

A history of the British freshwater algae by HASSALL (**3**) appeared in 1857. This well-known work contains descriptions of 42 species of Spirogyra under the name Zygnema. A single hint is given as to the time of year when conjugation takes place; namely, "The species of this group of confervae may be found in a state of conjugation during the entire spring, summer, and autumnal months, but more abundant in the spring."

In 1874 *The freshwater algae of the United States* by WOOD (**9**) was published in the Smithsonian Report. Speaking of the Zygnemaceae he says: "The family under consideration is among the commonest and most widely diffused of all the freshwater algae. They may be found in greater or less abundance at all seasons, but the spores appear to be formed only in the spring and early summer, at least these are the only times at which I have found fertile filaments. In the neighborhood of Philadelphia I have collected them in excellent condition as early as the beginning of April and as late as the latter part of June. Further south conjugation of course commences earlier, and fine specimens received by myself from Mr. CANBY were collected by him in Florida in February."

The work of PAUL PETIT (**5**) entitled *Spirogyra des environs de Paris* appeared in 1880. No general statement is made regarding the fruiting season of this genus, but, with one exception, dates are given with the description of the different species. These dates show that 20 of the 36 species described matured during March, April, and May; and all except two had matured by July. These were found

in fruit from July until October. One species fruited in April and May and again in October.

Since 1880 a number of papers relating to Spirogyra have appeared, but only a few of them give any facts that can be used in a study of periodicity. BENNETT and MURRAY (1) write: "Germination sometimes takes place while still in the mother cell; but most commonly both filaments perish after conjugation, with the exception of numerous zygospores which fall to the bottom. These remain dormant through the winter . . . . germinating in the spring . . . . instances are recorded of filaments persisting through the winter. HOFMEISTER states that the growth of Spirogyra is intermittent."

The following case is reported by W. and G. S. WEST (7): "We have melted out of the ice from Micham Common, Surrey, excellent examples of *Spirogyra catenaeformis* in conjugation, the vitality of which was in nowise impaired."

The few scattered remarks given include all the notes the writer has been able to gather from papers published before 1905. In this year a few papers appeared which had a more direct bearing on the subject at hand. These seem to be the pioneer publications on the subject of algal periodicity. In indicating some of the "problems of aquatic biology" FRITSCH (2) calls attention to the fact that different bodies of water, often far apart, will have the same dominant and often the same subordinate vegetation; also that a plant may be very abundant one month and almost, if not entirely, absent the next month. An intimate relation was found to exist between the relative abundance of an alga and its period of reproduction; the formation of the sex organs frequently preceding the disappearance or diminished abundance of a given species. FRITSCH writes: "In some cases no doubt these features (maximum abundance and period of reproduction) are influenced by the periodically recurring factors such as the rise of temperature and the increase in the intensity of light in the spring; so that the maximum abundance and period of reproduction are definite phenomena."

Another paper on the subject of algal periodicity appeared in 1905. So far the publications mentioned have had to do only with freshwater algae; for that reason it is well to call attention to studies made on marine forms. While at work on Dictyotaceae, WILLIAMS

(**8**) discovered that Dictyota had definite periods for the development of its fruit. This is well explained in his introductory paragraph: "While studying the development of the sexual cells in Dictyota, the interesting discovery was made that the process was practically simultaneous, not only for a given plant but for all the plants of the locality."

This work by WILLIAMS was done at Bangor, Wales, and at Plymouth, England. During the summer of 1906, observations were made on the same plant at Beaufort, North Carolina, by W. D. HOYT (**4**): "It was found at Beaufort, also, that this alga produced its sexual cells in regular, periodic crops. . . . . One observation is interesting in this connection. A female plant kept in the laboratory for nearly two months and then examined showed sori only slightly less advanced than those on plants growing in the harbor. . . . . This result is similar to the one observed by WILLIAMS but goes a step farther in showing that periodicity is transmitted to new structures formed from the original plant, even where these are not subjected to alternating conditions. . . . . It still remains to be seen whether the periodic habit can be transmitted through the protoplasm of the egg."

Spirogyra under artificial environment

In the laboratories in which these experiments were conducted, windows were used which faced toward the northwest, northeast, and southeast. Whenever a new line of investigation was begun, three sets of aquaria of different sizes were prepared. One set was placed in a northwest, one in a northeast, and one in a southeast window. The conditions made use of in the three sets of experiments were the same with the exception of a few degrees in temperature and a difference in light intensity. Other experiments were conducted which had nothing to do with conditions of temperature and light.

In the first experiments Spirogyra was brought into the laboratory and small amounts placed in aquaria filled with water from the pond from which the plant was taken. In some cases the plant was washed before being transferred to the aquaria, in others it was not.

A second group of experiments contained the same conditions

with the exception of the culture medium. In this group attempts were made to repeat the experiments while using tap instead of pond water. As a result, it was found that the aquaria with tap-water were as satisfactory, and, in most cases, much more so than those with pond water. Hence tap-water aquaria were used as controls.

It is well to note concerning this point that the tap-water was from reservoirs which were in turn supplied by small brooks and surface drainage. In many cases the pond water was taken from ponds supplied by brooks which drained the reservoirs just mentioned.

I next tried a group of experiments for the purpose of fixing some value to the use of plant food solutions for the investigation at hand. Knop's solution was most frequently used; however, Sachs's solution was employed in a great many experiments and in most cases simultaneously with Knop's. In comparing aquaria with and without food solutions, no general rule could be established. On the whole, however, the writer is inclined to favor at least a weak food solution. Knop's solution as low as 0.04 per cent. gave favorable results.

A long list of experiments was prepared in which rain and distilled water were used; and in others melted snow. Some of these were not disturbed after being placed in their respective windows. Others were left in these media for periods varying from one to ten days and then changed to a weak food solution (usually 0.05 per cent.), and this was raised by degrees to 0.2 per cent. where it was allowed to remain. In this group care was taken to select Spirogyra from different localities. Specimens were obtained from swift water, from slow-running brooks, and from small quiet pools and ponds where very little disturbance was possible. Notes on these experiments show that no particular advantage was gained by using these media.

From the first the aquaria located in the southeast windows were shorter lived than either of the other sets of aquaria. It will be remembered that the only difference in conditions was a slight difference in temperature plus a difference in light intensity. Experiments were now conducted in order to try the effect of shading the cultures. Tissue paper of different colors was used for this purpose. The best results were obtained when the aquaria were not shaded above the surface of the water. After scores of experiments the best results were obtained in the following way: when an aquarium was started,

it was shaded with black paper; after two weeks, this was changed to yellow; and after another two weeks the shading was not used at all. This was a decided advantage to the aquaria in the southeast windows. While the effect was not so noticeable in the other laboratories, the results were sufficient to justify this method in all the windows. It is not to be understood that tap-water aquaria were the only ones used with a shade. On the other hand, snow, rain, distilled water, and food solutions were used in every case. The same applies to the following series of experiments.

Up to this time no attention has been given to the substratum, nor to other plants with which Spirogyra is most frequently associated in its natural habitat. For this group of aquaria soil, débris, and plants, for the most part, were used from the immediate locality from which the specimens were taken. In some cases the soil was first sterilized.

Among the plants which seemed beneficial to Spirogyra, none proved more helpful than Oedogonium. In fact in every aquaria in which Spirogyra lived for several months or a year, Oedogonium was invariably present and often the predominating alga. The Oedogonium could usually be found attached to the sides of the jar or floating at the surface, thus shielding the Spirogyra from too much sunlight. Chara supplied to the aquaria was helpful so long as it was not too abundant. In some cases where aquaria were thus started, the Chara died out after two or three months and was followed by an abundant growth of Oedogonium, and later by Spirogyra. In the field, masses of Spirogyra were often collected among water cress, but in no case was a good growth of Spirogyra obtained in an aquarium with this plant. A number of jars were supplied with oak leaves taken directly from the trees where they had remained all winter. To other aquaria pieces of charcoal were added. Both of these factors seemed beneficial and in most cases excellent cultures of Spirogyra were obtained which lasted until conjugation had taken place.

Spirogyra under natural environment

Field-work was begun early in April. At this time 400 aquaria of all sizes were in use and 100 of them contained excellent cultures of Spirogyra which had been under cultivation for two months. On

April 27 *S. quadrata* was found conjugating abundantly. This one was followed by others until twelve different species had matured and disappeared. At first all material was brought to the laboratory in small jars and then examined, but this method was by no means satisfactory. A microscope together with a crude temporary stand was added to my collecting outfit, and an examination of all material was made on the spot. There are so many chances of collecting worthless material that no other method was found which would give definite results.

The first task was to locate Spirogyra in a number of different localities with different conditions of environment. Accordingly a few localities were selected varying from a few rods to twelve miles apart. Within these regions 40 different places were selected which could be visited frequently and studied with care. Some were in open places, while others were in deep shadow; some were in pure running water, others in filthy stagnant pools; some with numerous other algae, others almost alone; and under many other conditions.

For identification of species some of the material was usually killed in the field as soon as collected. From 2 to 4 per cent. solution of formalin was used for this purpose when larger masses were killed, but in most cases chromacetic solution was used according to the formula given in CHAMBERLAIN'S *Methods in plant histology*, p. 139 (chromic acid 1^{gr}, glacial acetic acid 4^{cc}, water 400^{cc}). Several stains were used, but Haidenhain's iron-hematoxylin was most satisfactory. Some of the specimens stained in this way were afterward mounted in glycerin, others in balsam, and others in Venetian turpentine. I found the balsam more satisfactory than the turpentine, but excellent preparations were obtained by using the Venetian turpentine method recommended by CHAMBERLAIN (stain with magdala red and anilin blue and mount in Venetian turpentine). Stained preparations in glycerin were most quickly obtained by taking the material as soon as washed from the chromacetic solution, transferring it to a 10 per cent. solution of glycerin to which was added 2 or 3 drops of Ehrlich's blood stain, and allowing it to concentrate. In some cases the stain obtained by this method has been permanent, in others it has faded after a few months. This method

of preparation has been used with much success by F. N. DUNCAN and O. P. DELLINGER, of this laboratory, for animal tissue.

Periodicity of species studied

For the purpose of identifying the different species, the following authors were consulted: VAUCHER (**6**), WOOD (**9**), PETIT (**5**), and WOLLE (**10**). A brief account of the fruiting season of the different species will be given below.

Spirogyra inflata (Vaucher) Rab.—VAUCHER reports this species in fruit from February 20 to March 19. PETIT gives April–May. Unfortunately I was not able to find it except in a single locality. This was in a small pond covering an area of perhaps $1000^{sq.\,ft.}$. The surface was well covered with algae and floating débris of small sticks and grass. This species was found floating on the water together with *S. catenaeformis* and *S. calospora*. On May 2 all three species were found in a state of conjugation interwined with each other. No indication of *S. inflata* was found after May 12, although this pond was visited frequently during the summer and fall.

Spirogyra quadrata (Hassall) P. Petit.—This is the *Zygnema quadratum* of HASSALL. PETIT gives the fruiting season as April–May. The writer studied this species in eight different localities, varying from a few rods to twelve miles apart, but under no great variety of conditions. In every case it was found in quiet surface-water pools or streams which were entirely dry by the middle of July. All the eight places were in low pastures or meadows and specimens were collected from among dead grass and leaves. *S. quadrata* was found fruiting abundantly April 27, and within a week the eight places mentioned above were visited and found in about the same state of conjugation. By May 5 the Spirogyra at two localities had fruited abundantly and had passed the maximum of conjugation. By May 12 this was true in every case and no fruiting material was found after May 19. The temperature of the water recorded at each visit to the different ponds gave a range of 10–25° C. It was very difficult to collect any vegetative filaments of this species after the period of maximum conjugation had passed.

Spirogyra calospora (Cleve).—WOOD found this species fruiting in a ditch in a meadow late in April, and as late as May 25 in the

"neck" below Philadelphia. The season given by PETIT is April–May, and the habitat "ditches in low ground and swamps." For this species the present paper includes notes from observations of five different ponds and one brook in different localities, and including a greater variety of conditions than those described for *S. quadrata*. Early in April the plant in question was growing abundantly and continued in increasing abundance until about the second week in May. In two of the ponds the disappearance was by no means rapid. A few scattering filaments were found May 6 and the last June 4. The average temperature was 7–14° C. In the pond in which most fruiting material was found the temperature ranged from 7 to 11° C at the time of maximum conjugation.

Spirogyra Hantzschii Rab.—In 1906 fruiting material was collected first on April 28, and, with one exception, no fruiting material was gathered after May 23. In the fall of 1905 this species was found in active vegetative condition in three localities. Examinations were made frequently during the fall and, when the ponds were free from ice, during the winter. This species lived beneath the ice and in two of the three localities the plant did not come to the surface at the time of conjugation, but was collected from the débris at the bottom of the ponds. Temperature of the water varied from 12–28° C. There was no great range of habitat; generally in shallow ponds near the mouth of a small stream, and more or less protected from the midday sun.

Spirogyra mirabilis (Hassall).—This species is described by HASSALL and also by PETIT as producing spores without conjugation and by no other method. WOLLE states that lateral conjugation is more frequent than scalariform. I was not able to find this species in fruit in the pond from which this material was taken. It was brought into the laboratory in the vegetative condition April 2 and within a week was fruiting in several aquaria. On May 7 a few filaments with scalariform conjugation were found; all other spores were formed in cells where no conjugation had taken place. Comparatively few cells formed spores and very few cells conjugated. PETIT gives March–July as the fruiting season. In the material mentioned all fruiting specimens had disappeared in all the aquaria by the second week in June.

Spirogyra Jurgensii (Ktz.).—This species was found in fruit in the neck of a small pond May 4, 1906. In the same locality were found vegetative filaments of *S. Hantzschii* and Oedogonium, besides sticks, dead grass, rusted wire, and tin cans. The algae mentioned were found here in small patches January 8, and were visited at least once each week until June, at which time no algae of any kind were present. The fruiting specimens were most abundant when the temperature averaged about 12° C., and lasted about a week. No fruiting specimens were found after May 25. PETIT gives the conjugating season as April–May.

Spirogyra catenaeformis (Hassall) Ktz.—This species, so far as I know, has not been reported for this country, and is so placed because it corresponds so closely to the descriptions in the works of HASSALL and PETIT. The latter author gives the fruiting season as April–May, and the habitat "very humid ditches, wooded ponds, etc." The first fruiting material was collected May 4 and the last May 22. It was found in two localities about two miles apart. One was a shallow ditch and the other was in cow tracks near a small stream. The period of conjugation was the same for both localities. The temperature of the water ranged from 14 to 17° C. This species was found with *S. dubia* in one pond and with *S. inflata* and *S. calospora* in another pond.

Spirogyra varians (Hassall).—This plant was studied in five localities from one to eight miles apart. In one case the water was rather swift and the Spirogyra was fruiting wherever it happened to lodge against a support. The other localities were shallow ditches and ponds. The first fruiting material was collected May 2, and the last May 23. In all localities except that in swift water this species fruited abundantly. The average temperature of the water was 8–12° C.

Spirogyra longata (Vaucher).—For this species my observations were confined to two ponds about one mile apart. In one *S. longata* covered an area of perhaps 200 sq ft and in the other fully 100 sq. rods of surface. In both ponds the plant in question was well exposed to bright sunlight, receiving its main protection from numerous algae which were present. The temperature of the water ranged from 20 to 25° C. and the depth of the water from a few inches to

several feet. VAUCHER says that this species conjugates from February 20 to April 12; PETIT gives April–May. In the ponds mentioned this species appeared in July and with increasing abundance until early in August. The first fruiting specimens were collected August 2, and the last August 21, and neither vegetative nor conjugating filaments as late as September 1.

Spirogyra Lutetiana (P. Petit).—I was not able to identify this species except in a single locality. Its habitat was a small open ditch in a meadow unprotected from the sun. PETIT gives the fruiting season as March–May. The only date at which I found it in a state of conjugation was October 14, and when collected it had all the appearance of being old material which had fruited earlier. This may have been a week and it may have been a month.

Spirogyra dubia Ktz.—Concerning this species WOOD writes: "I have found this species fruiting abundantly in May. When in this condition it forms a mass of dirty yellowish-green." WOLLE agrees as follows: "Fruiting abundantly in May; forming dirty yellowish-green masses." I have found this species in fruit in seven different localities. The first date for each was as follows: May 1, May 2, May 21, July 31, July 31, August 10, and August 10. Those fruiting in May were found in rather sluggish streams and in water varying in depth from one to four feet; those fruiting in July and August were in cattle tracks and in a small ditch. The conjugating period in the spring lasted about four weeks; in the summer the period was about two weeks. The temperature of the water in the former ponds varied from 12 to 18° C.; in the latter places from 22 to 28° C. All seven localities were situated where the plant was protected from direct sunlight for a part of the day.

Spirogyra orthospira (Nägeli).—I had an excellent opportunity to watch the life-history of this species in a small pond of about 100 sq ft in area, two to four feet deep, and well shaded with low alders. The surface of the pond was entirely covered with Spirogyra to a depth of several inches. On May 22 it was found to be fruiting abundantly both at and beneath the surface. It reached its maximum about the second week of June, and by June 30 either vegetative or conjugating filaments could be found only by examining the débris at the bottom of the pond.

General conclusions

In forming conclusions concerning whether any given plant passes through a series of regular recurring phenomena, it is well to withhold positive conclusions until the plant in question has been carefully observed for a number of successive seasons. This method of approach becomes more complicated, but at the same time safer, if the plant can be studied from a number of varying conditions of environment. However valuable external conditions may be in effecting any given phenomenon, it seems well not to overlook whatever influence may be due to internal conditions. There may be conditions that cannot be seen, felt, weighed, or measured, that initiate and support even the simplest plants through a series of complicated phenomena. Notes on Spirogyra for this region seem to credit much influence to internal conditions. Here were forty different places in which this plant appeared, matured, and disappeared, in a single season. Without a single exception the disappearance was immediately preceded by a period of conjugation. Special importance is given to the fact that in no case did all of the filaments enter into spore formation either with or without conjugation. It is to be further noted that both the vegetative and conjugating filaments disassociated almost at the same time and disappeared, even from places where this plant was abundant over comparatively large areas of surface.

Of the twelve species studied, ten were in fruit in May, and in every case the maximum abundance of conjugation occurred within this month. In a few places more than one species was in fruit at the same place and time, but usually if several forms grew together they conjugated at different times, their period of maximum conjugation succeeding one another at intervals ranging from one to two weeks. For example, early in March, within a distance of forty rods, four species of Spirogyra were found growing together at three different places at the edge of a slow brook. In two of the three places Spirogyra was very abundant and covered an area in each of about 200 sq ft. Probably all had had the same source earlier in the year during high water, but remained distinct until all had disappeared in June. No fruiting material was found in either of the larger patches; two of the four fruited in the smaller one, but not at the same time.

S. Jurgensii was found in fruit May 1–May 15; *S. dubia* was found fruiting May 21–June 4.

Under the description of *S. inflata* mention was made of the fact that on May 2 this species together with *S. calospora* and *S. catenaeformis* were found in fruit at the same time and place. It ought to be noted, however, that *S. inflata* had passed its period of maximum conjugation and that there were comparatively few filaments of either of the other two species. No *S. inflata* was found after May 4, but from this until May 22, *S. catenaeformis* was abundant. In giving a description of the latter species it was noted that this form was found fruiting abundantly at the same time and quite near *S. varians*. I did not find the two species intermingling, although growing abundantly almost in the same mass and having the same fruiting season.

I am inclined to think that not enough emphasis is given to the fact that the lower plant forms do not have a continuous period of growth, either vegetative or reproductive. In other words, the normal period for either activity is continuous for only a few weeks or months at most; it remains a problem of research to show how inclusively this generalization applies to the freshwater algae. For Spirogyra the observations reported in this paper seem to offer overwhelming evidence in support of the view, for this region at least, that it is not a perennial plant. I have only a single exception to this conclusion and will speak of it later. A few of the species studied appeared more or less abundantly in the fall; in this connection *S. Hantzschii* furnishes a specific example. In a majority of the forty localities kept under observation during 1905–6, several forms of algae succeeded one another in maximum abundance in the course of a year. In only four of the forty places was any trace of Spirogyra found in the fall where it had been in a state of conjugation in the spring. The manner in which different species appeared, matured, and conjugated was for most of the forms quite distinct and constant for the several localities. Following the fruiting season the disappearance of the plant took place sometimes suddenly and sometimes gradually.

It is a well-known fact that vegetative material is very difficult to identify; the same might as well be said of conjugating material. For this reason it is difficult to follow any given species with certainty;

where several closely allied species are associated, this is practically impossible. Fortunately this did not occur except in a few places. However uncertain and unreliable may be one's observations and conclusions relative to a given species during its period of vegetative growth, it is possible to determine with some certainty whether or not the different species of Spirogyra have any definite or fixed periods at which they conjugate, or whether this phenomenon takes place only under certain conditions of environment. In all cases notes were taken at each visit to a pond, and the determination of the species left until the fruiting season; then by going back to my notebook, the life-history could be worked out with some certainty. Leaving out of account uncertain conditions such as the vegetative activities, and placing special importance on the period at which conjugation takes place, it is possible to conclude that one of the two important phenomena (vegetative and reproductive activities) in the life-history of this alga appears periodically, not due exclusively to seasonal conditions nor to environment.

No one can say with absolute certainty whether the natural forces that produce conjugation are internal or external. It is a fact, however, that whenever a condition was present, in any part of a mass, which was able to initiate and control reproductive activity, there was at the same time and place either the same or some other condition which brought about the destruction of all vegetative filaments. In this study no exception was found to this rule, whether under laboratory or under natural environment.

Up to the time when conjugation was abundant in ponds, brooks, and ditches, I still had over 300 aquaria in the laboratory. A small percentage of them contained fruiting Spirogyra. The time of fruiting for any given species began about one week earlier and lasted about one week longer in the laboratory than that of the field. The disappearance of the vegetative filaments was also more gradual. It was not difficult to keep aquaria early in the year, but after the middle of May they began to decline and were kept only with increasing care until mid-summer, when out of 700 only one remained.

As to the different sizes of aquaria, it ought to be said that some were ordinary test-tubes; some contained 25–30 liters; and the majority ranged from one to ten liters. The results were not constant

for either the large or small sizes, although all sizes were usually arranged at the same time. In dozens of test-tubes two-thirds full of water or culture media Spirogyra kept well two to three months. On the average, however, aquaria of four to ten liters were most satisfactory. In three large aquaria of about forty liters each no successful cultures were made, although frequently attempted.

An attempt was repeatedly made to grow Spirogyra in some of the larger aquaria after a species had died in it and without renewing the culture media. In every instance where this was tried the plant died down in a few days, showing that the solution contained a toxin injurious to Spirogyra. It is left as an open question whether a mass of Spirogyra in nature dies from the accumulation of this same destructive element.

Aside from the twelve species herein described, there was still another which has been kept under observation since early in the fall of 1905. It is a large form and was found growing in rather large bright-green patches in the running water of three different brooks one to three miles apart. When first found, a few aquaria were started, one of which has remained to the present time without any indication of decline. This is an ordinary aquarium of about 10 liters; it is kept well covered and for that reason very little evaporation takes place. The main algal associate is Oedogonium, and a few brown and green hydra have lived in the aquarium from the beginning. This jar is the one exception to the 700 aquaria that died down during the season of 1906. In concluding, I wish to call attention to the fact that no trace of a conjugating filament has been found in this aquarium; and furthermore, that none was found at any of the three brooks mentioned, although in one case the plant was very abundant. It is also remarkable that there has not been a time from the first when vegetative specimens of this species could not be obtained.

In addition it ought to be said that this study was continued during the following year (1906–7), in the same locality, under about the same conditions and methods of study. This second year's observations and experiments did not vary enough from those of the previous year to warrant any change in the conclusions above given.

Summary

1. Few of those who have published papers on the genus Spirogyra have given any notes on the subject of periodicity.

2. Out of 700 aquaria it was found that the best way to arrange a culture was to place some sterilized earth in the bottom, add some dead leaves or dead grass, allow to settle well, then add a small amount of Spirogyra, and place at first in a window not exposed to direct sunlight.

3. Of 300 aquaria in the laboratory at the time when Spirogyra was fruiting most abundantly under natural conditions, there were about 5 per cent. which contained conjugating material. The time corresponded with that of the field.

4. Leaving out of account the number of species which may have been collected in the vegetating condition and for that reason doubtful of identification, there were at least thirteen different species collected, of which twelve fruited more or less abundantly.

5. Ten of the thirteen species passed their period of maximum abundance in May, one in August, and one in October. A few doubtful fruiting filaments of *S. Hantzschii* were found a second time in August. The only reliable example of a second fruiting period found was *S. dubia*, which fruited in May, and again in small patches, but relatively abundant, during the latter part of July.

6. When field-work was first begun, material was collected and then brought to the laboratory for examination. This method was by no means satisfactory and for that reason was discarded. All the later collections were examined on the spot with a microscope.

7. The period of maximum abundance corresponds in every case with the period of maximum conjugation. The decline of one was always accompanied by that of the other.

8. After conjugation had ceased the fruiting filaments disappeared more or less gradually. The vegetative filaments also disappeared, and at the same time as those containing zygospores.

9. In the laboratory no Spirogyra was found fruiting at the surface but always near the substratum. In the field the reverse was true. *S. orthospira* and *S. Hantzschii*, however, were prominent exceptions.

10. Of the thirteen species one has not been found in a state of conjugation. It has been kept under observation, in excellent con-

dition, both in the laboratory and in the field, since October, 1905, but no trace of fruiting material has been found.

11. Notes taken in the field and supplemented by those in the laboratory offer overwhelming evidence in support of the view that the phenomenon of conjugation results not so much from external as from internal conditions.

12. The writer therefore concludes that Spirogyra has definite periods of growth and activity.

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ON THE POLLEN OF *MICROCACHRYS TETRAGONA*

ROBERT BOYD THOMSON

(WITH PLATES I AND II)

"*Microcachrys tetragona* occurs only on the highest summits of the Western Range and Mount Lapeyrouse in Tasmania. It was introduced to the Royal Gardens at Kew about the year 1857 by Mr. WILLIAM ARCHER, on whose property it grew. Although of great interest in a botanical sense, its only value as a garden plant is for conservatory decoration, for which the elegant habit it can be made to assume under pot culture, its neat foliage, and bright-red fruits render it highly suitable."[1] The specimens for this work were obtained through the kindness of the present director of Kew Gardens, Colonel PRAIN, whose courtesy and that of the staff is much appreciated by the writer.

The general features of the fruiting branches of microsporangiate and megasporangiate plants are indicated in *pl. I*. The cones are borne terminally and their sporophylls are spirally arranged, in contrast to the opposite and slightly concrescent vegetative leaves (*pl. I*, and *pl. II*, *fig. 1*, the branch to the left).

The microsporophylls bear two somewhat spherical, pendant sporangia (*fig. 2*), whose form and structure, after the discharge of the pollen, is indicated in *figs. 3* and *4*. The terminal scale of the sporophyll is broadly triangular in outline (*fig. 2*), very much extended dorsally (*fig. 3*), but not, or scarcely at all, in the ventral direction. The inner layers of the wall are much collapsed at the stage indicated, but the epidermis retains a very definite structure on account of its peculiar thickened bands. These are shown in transverse and in longitudinal section in *figs. 5a* and *5b*.

In *fig. 4* some linear and branched structures are apparent in and around the sporangia. These are the hyphae of a fungus, and to their presence the retention of many of the pollen grains in the dehisced sporangia of my material is due. The hyphae are often

[1] KENT, ADOLPHUS H., Veitch's manual of Coniferae 161. 1900. The references to the discovery of this form and its description are given here.

in intimate association with the pollen, they frequently branch, and the branches form contact with the grains. This pollen is no different from the less abundant found in uninfected sporangia.

The pollen of Microcachrys (*fig. 8*) is small as compared with that of Saxegothaea (*fig. 9*), Podocarpus (*fig. 10*), or Pinus (*fig. 11*), all these figures being the same magnification for the purpose of comparison. The grains vary considerably in size, a feature which my material of Saxegothaea also shows. They are winged, though in some instances I have thought that no wings were present, but more material was needed to determine this point than was at my disposal. The wings arise in the ordinary way by a separation of the exine from the intine. In longitudinal section the grains usually show two rather poorly developed wings (see various grains in *fig. 6*), and in following the series these two are often all that one can be certain of. In gross material, however, three wings are readily apparent (*fig. 8*).[2] In transverse sections, also, which pass through the ventral part of the grain, the three-winged condition is clearly seen (see middle of *fig. 6*). In some cases one of the wings is very small (*fig. 6*, grain in upper part of the field). The lowest grain in *fig. 6* shows the presence of four wings (the central one very dark). Some four-winged grains have one pair of wings much smaller than the other. Exceptionally, five and six-winged grains are found. A student, Mr. W. P. THOMPSON, kindly made a careful determination of the number of wings in gross material from several cones, rolling the grains in fluid under the cover glass. He found that of sixty-four grains, fifty were three-winged, three of these having one very small wing; nine were four-winged; two had five, and three had six wings. The pollen studied was in the mature condition and the wings must have been fully developed. *Fig. 7* shows the greatest expansion of the wings that I have observed. They usually do not extend laterally beyond the body of the grain (*fig. 8*, also some grains in *fig. 6*). They project, however, beyond the body of the grain ventrally, though not to such a degree in either direction as do those of Podocarpus (*fig. 10*) or Pinus (*fig. 11*). A small amount of material from the apex of one of the cones showed another feature. When the

[2] I studied the grains in section first, and this led me to misinterpret the number of the wings, as stated in BOT. GAZETTE **46**:465, 466. 1908.

pollen grain has a five-celled gametophyte, the wings are very small, not much larger than they are in Pinus when its pollen is still in the tetrad condition. The wings of Microcachrys arising thus late ontogenetically give indication of their recent acquirement.

With regard to the microgametophyte, I find that in the mature condition of the pollen four prothallial cells are often present, though three are more usual. When three only are present, it is the second prothallial cell that has divided (*fig.* 7). The first and second prothallial cells have walls which turn blue with chlor-iodide of zinc. No further cellulose walls were demonstrated. *Fig.* 7, in addition to the prothallial cells, shows a lateral derivative of the body cell and the tube nucleus. The gametophytic structure thus conforms to that which recent investigators have shown characterizes the related forms. Perhaps it is not out of place here to give credit to THIBOUT,[3] the first person, so far as the writer knows, to describe and figure a multicellular gametophyte in the Podocarpeae.

NORÉN in his recent work on Saxegothaea[4] has emphasized the relationship of this form to the Araucarieae. He finds that, in addition to the supernumerary prothallial cells, there is a curious reminiscence of this group in the mode of pollination, the pollen sometimes being deposited in the cavity around the ovule and growing over the tissue into the micropyle, a condition which so far as can be judged is essentially similar to that which I have found in Agathis. He also calls attention to the wingless condition of the pollen in both Saxegothaea and the Araucarieae.

With the present contribution our knowledge of the occurrence of excess prothallial tissue in all genera of the Podocarpeae is complete. The winging of the grain in Microcachrys is of varied and indefinite character, late in development, and undoubtedly of primitive type, the form occupying in this respect an intermediate position between Saxegothaea on the one hand and Dacrydium and Podocarpus on the other. This is the more evident from the presence of three wings in some species of Podocarpus. THIBOUT describes the

[3] THIBOUT, E., Recherches sur l'appareil mâle des gymnospermes. pp. 265. *pls.* *16.* Lille. 1896. See *pl.* *14*, *figs.* *8* and *9*, of *Podocarpus polystachya.*

[4] NORÉN, C. O., Zur Kenntnis der Entwicklung von *Saxegothaea conspicua* Lindl. Svensk. Bot. Tidskr. **2**:101–122. *pls.* *7–9.* 1908.

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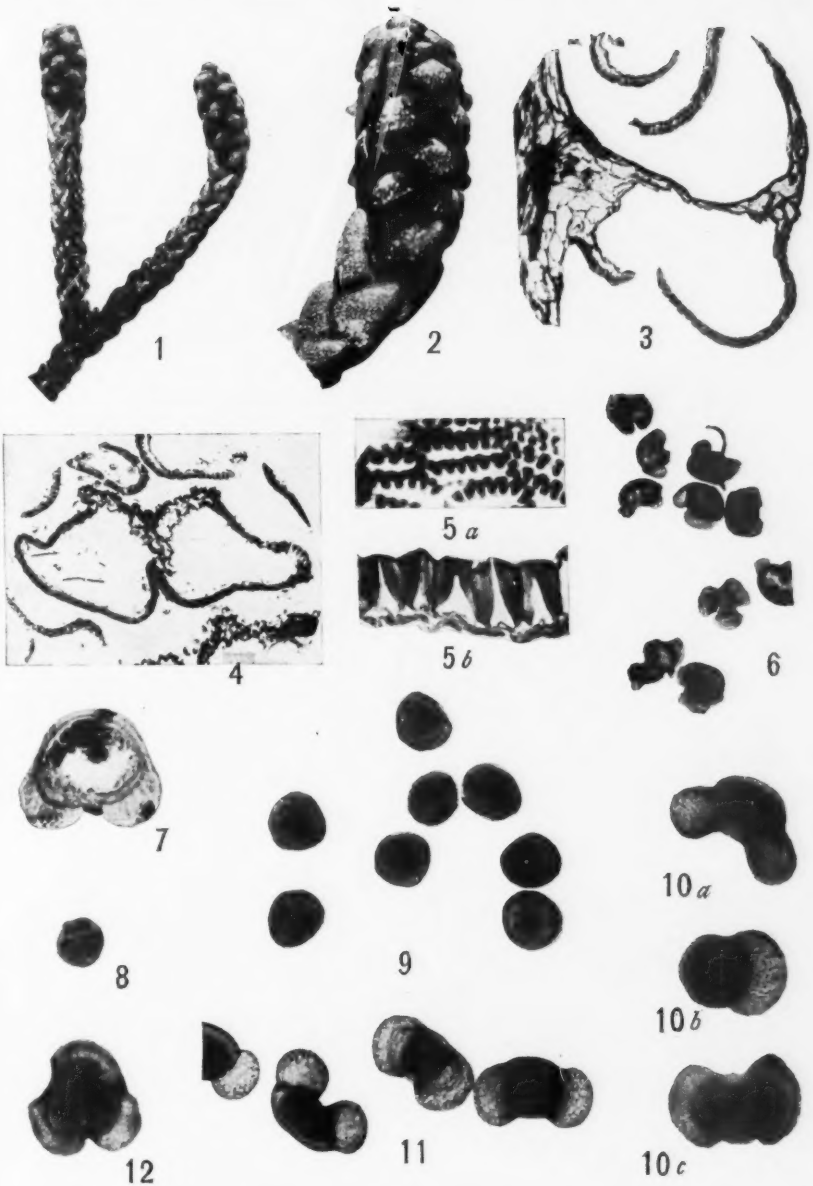

THOMSON on MICROCACHRYS

pollen of *P. dacrydioides* as having normally three wings (*op. cit., pl. 14, figs. 10, 11*). I have found three wings present exceptionally in the usually two-winged *P. ferruginea* (*fig. 12*). Unfortunately, no data nor material of the more probable genus Dacrydium were available.

The bi-winged condition of the pollen on the pines and podocarps has often been referred to as an indication of affinity between the groups. This view has no longer support, since the winging of the grain has arisen in the Podocarpeae within the group itself, and so is distinct from that of the pines. In a further contribution on the character of the megasporophyll of Saxegothaea and Microcachrys, the writer hopes to show the essential difference of this structure in the two great phyla of the conifers.

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EXPLANATION OF PLATES I AND II

PLATE I

Twigs from staminate and ovulate plants. ×2.25.

PLATE II

FIG. 1.—Branch with microsporangiate cones. ×4.

FIG. 2.—One of the same enlarged; the sporangia can be seen in pairs beneath the terminal scale of the sporophyll. ×9.

FIG. 3.—A microsporophyll in longitudinal section, to one side of the axis.

FIG. 4.—Same in transverse section; the linear structures in the sporangium are the hyphae of a fungus shown in contact with pollen grains in *fig. 6*.

FIG. 5*a*.—The wall of the microsporangium in tangential section.

FIG. 5*b*.—The same in transverse section.

FIG. 6.—A field of sectioned pollen grains; below is one with four wings; above it one with three wings cut transversely and a small part of the body uniting these; various other aspects of the wings.

FIG. 7.—The microgametophyte.

FIGS. 8–11.—Pollen grains at same magnification: *fig. 8*, Microcachrys, from below; *fig. 9*, Saxegothaea; *fig. 10*, *Podocarpus ferruginea* (*a* and *b* two latera views at right angles; *c*, dorsal view); *fig. 11*, *Pinus resinosa*.

FIG. 12.—A three-winged grain of *Podocarpus ferruginea*.

A VEGETATIVE MUTANT, AND THE PRINCIPLE OF HOMOEOSIS IN PLANTS

CONTRIBUTIONS FROM THE AMES BOTANICAL LABORATORY, NO. 9

ROBERT GREENLEAF LEAVITT

(WITH NINETEEN FIGURES)

When viewed in their relations to morphogenetic and broader evolutional problems (as distinguished from narrower phylogenetic, or genealogic, problems) numerous facts of teratology—a descriptive cult without unifying principles, heretofore pursued chiefly by the vaguely curious, and lending itself discreditably with equal readiness to either side of many a morphological discussion in the past—manifest a special and high value. The production of form from formlessness in the egg-derived individual, the multiplication of parts and the orderly creation of diversity among them, is an actual evolution, of which anyone may ascertain the facts, but of which no one has dissipated the mystery in any significant measure. This microevolution forms an integral part of the grand evolution problem and lies at the base of it, so that we shall have to understand the minor process before we can thoroughly comprehend the more general one. Morphogenetics, therefore, is a field in which the evolutionists must work. The development, or morphogenesis, of a single individual—if it be such a case as may improve our insight into the nature of the ontogenetic process micromechanically considered—may be of as great interest in the eyes of the evolutionist as the origin of a new race or the fate of an old one.

It is this relation, to the central rather than the peripheral problems of evolution, which has led me to carry out certain observations upon abnormalities in plants. Yet I shall try to make clear, also, the bearing which some of the observed individual variations have upon types of racial variation. In this connection some facts of normal, i. e., established, morphology will be noticed. The main principle under discussion seems to deserve a place, though a minor one, in any complete account of the evolution of species.

The present paper is sequel to a casual observation made several years ago, when as I was passing near a horsechestnut tree in the autumn I noticed, upon a depending branch, a leaf which had lost several of its leaflets. I found that the palmately compounded leaves of this species fall to pieces as they are cast off by the tree, or even before this event. The leaflets are removed as if by a clean cut; and sometimes the petiole, quite devoid of blades, is left standing alone upon the stem.

This complete dismemberment seemed to me a curious thing. Abscission at the base of the petiole is not a simple decay, but is, as everyone knows, a somewhat complicated process, wherein there is formed across the leaf-stalk, through suitable cell divisions, a plate or layer of cells, by the disintegration of which the leaf is ultimately allowed to fall away. The cell walls of the scar-surface become suberized, so that the wound is sealed against the loss of water. Leaf-abjection is thus a complex adaptive process.

The question arose, Why should the abscission proper to the petiole-foot be repeated in all of its details at the bases of the petiolules?—for I ascertained that the process is carried out in full at these points in this species. Of what use to the tree is it that the frame of the leaf, now emptied of its valuable contents which have been withdrawn into the stem, should be carefully disarticulated? I have never been able to imagine any utility nor have those to whom I have propounded the riddle suggested any. I believe that in fact the habit is neutral in the tree's economy.

If this is so, the evolution of absciss-layers in petiolules cannot be referred to natural selection. For in the plan of evolution by the accumulation of variations under the guidance of natural selection, developing organs must pay their way as they go.

An explanation of the presence of the useless structures occurred to me. It seemed probable that the absciss-layer perfected in the natural course of evolution at the foot of the leaf-stalk had, subsequently to the compounding of the blade in this species, been transferred, so to speak, to the bases of the petiolules. The disarticulations of the leaflets seemed to be a series of ecologically meaningless echoes of the primal, useful disarticulation at the junction of stem and petiole.

The horsechestnut is not peculiar in this respect, and further considerations, with regard to compound leaves generally, have confirmed in my own mind my first understanding of the matter. Disarticulation of the leaflets seems to be universal in deciduous-leaved species. It occurs in many families separated in a natural system by entire-leaved groups, as in Juglandaceae, Berberidaceae, Anonaceae, Rosaceae, Rutaceae, Sapindaceae, Vitaceae, Oleaceae, Bignoniaceae, Caprifoliaceae. That is, it must have arisen in evolution many times independently. There must, then, be some wide underlying principle capable of bringing the disarticulation in question to light, wherever compounding of the blade establishes the conditions for its operation. This principle seems, as has been argued above, not to be natural selection. There is, however, in plants a recognizable principle of morphic translocation, mobility of characters, or *homoeosis* (BATESON), to which the phenomenon may very well be referred.[1] The conditions favorable to its operation in this case are very obvious, since the structural relations at the junction of the petiole and stem are imitated at the junction of petiolule and petiole (or rhachis).

The Pierson fern

Recently evidence corroborating the above interpretation has come to hand in a case where advance in complexity has been all but observed. In the title I have alluded to it as a case of mutation; but perhaps I am using the word somewhat loosely, if the DeVriesian sense is to be insisted upon. The plant is the Pierson fern, now well known to horticulturalists and to the public generally. The metamorphosis of the Boston fern, to which the Pierson owes its origin, seems not to have been hitherto described as a homoeotic transformation; yet such it is.

The first plant of the variety was found while it was still small, among vegetatively propagating Boston ferns in the greenhouses of Mr. F. R. PIERSON, the well-known horticulturalist of Tarrytown-on-Hudson, N. Y., in 1900.[2] While it was not a "pedigreed" plant,

[1] My first paper on this topic, entitled "On translocation of characters in plants," appeared in Rhodora 7:14–19, 21–31. 1905. When it was written I did not know that BATESON had briefly treated the same subject in relation to variation of animals and had devised the name homoeosis. I find his term applicable to the present purpose and more convenient to use than my own expression.

[2] Mr. F. R. PIERSON, in a letter to the writer.

its derivation is patent, for when its descendants are grown under poor conditions, they generally revert temporarily, in a part of their fronds at least, into the primitive state, which is seen to be that of the Boston fern. This constitutes highly desirable proof of parentage. Whether the sudden alteration of character took place in a spore, or in a bud from a runner, is not surely known. Nevertheless the circumstances leave little doubt on this head; for the Boston fern, while richly stoloniferous, is almost universally sterile. Mr. PIERSON believes the original individual to have been a bud-sport. The young plant caught the eye of a gardener, who brought it to the notice of Mr. PIERSON, and it was set aside so that its development might be followed. All Pierson ferns and numerous varieties have descended from this individual.

In this case we may say that the transformation, which affects the leaves of the fern and consists not in the introduction of altogether novel outlines or proportions, but rather in the relocation of forms already in existence, has taken place under observation. A single individual has been noted to emerge from the common mass—under cultivation as an isolated colony—with very markedly altered characters. New features have not been slowly developed through several generations, but have appeared suddenly.

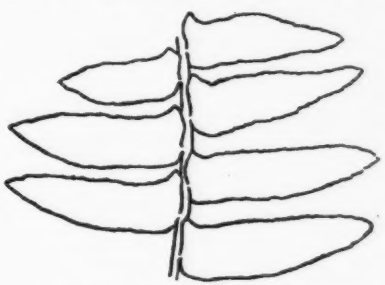

FIG. 1.—Pinna of Boston fern.

The Boston fern has simply pinnate fronds. The pinnae are entire, serrulate-margined, oblong, and usually bluntly toothed or auriculate on the upper margin at base (*fig. 1*). In the new plant, the pinnae have become divided,[3] and at the same time elongated—often much elongated. Their divisions, the pinnules, are oblong and, when fully developed, toothed or auriculate on the upper margin at base (*fig. 2*). The pinnules, in fact, are very good copies of the

[3] When the new form is fully expressed. The division may affect only part of each pinna.

original pinnae; and if we lay a well-developed pinna of the Pierson fern by the side of a small frond of the Boston fern, we shall be struck with the fact that they are almost identical. In short, the

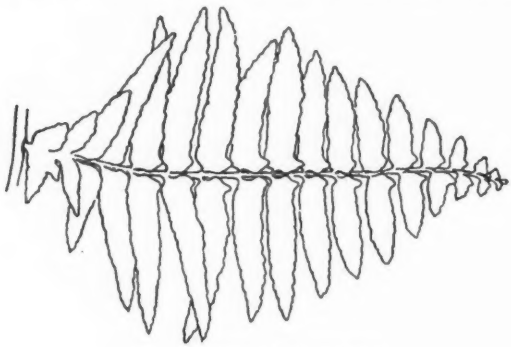

FIG. 2.—Pinna of Pierson fern.

pinnae of the new variety are transformed from the original condition in such a way that the plan of the whole frond of the Boston fern is now seen in the primary segments of the Pierson frond.

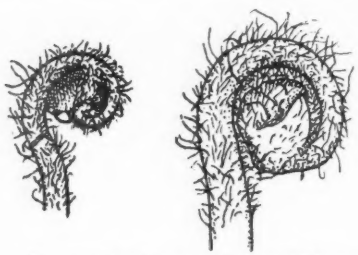

FIG. 3.—Growing apex of pinna of Pierson fern (left) and Boston fern (right).

The completeness of the imitation may be indicated still further:

1. The pinnae are elongated, the growth being less strictly determinate than that of the original pinnae, and more like that of the frond.

2. The apical growth of the pinnae is now circinnate, as shown in *fig. 3*, after the fashion of the original frond. The pinnae of the Boston fern on the other hand, while lapped together in the young state at the summit of the developing frond, are not in the least circinnate.

3. The blades of the pinnae are divided.

4. The outline of the pinnules is like that of the original pinnae.

5. Finally, the peculiarity of the original form, that its pinnae in age become disarticulated by the development of an absciss-layer,

and ultimately fall off after several layers of brown tissue have been developed on the scar surface-to-be, is now shown by the pinnules of the Pierson fern. The pinnules of the latter are discovered to be deciduous, and a minute investigation shows that deciduity is secured by the development of an absciss-layer at the base of the pinnule, with the formation of brown scar-tissue. Thus the translocation of the structures concerned in disarticulation of leaflets is in this case an ascertained occurrence: these structures have passed at once and unaltered from the bases of the pinnae to the bases of the pinnules.

The beautifully soft and luxuriant aspect of such ferns as the Whitman[4] is due to the fact that each frond is in effect made up of

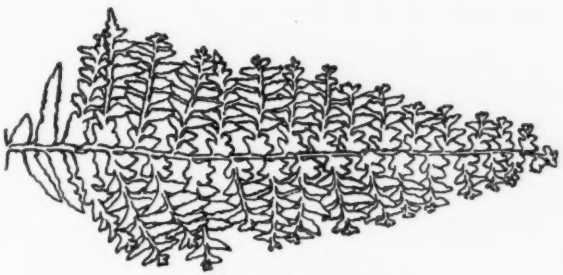

FIG. 4.—Pinna of Whitman fern.

many small fronds. In this last-named variety, and in some others, as Pierson's *elegantissima* and *superbissima*, homoeosis has gone one step farther than in the Pierson, so that we find a thrice-compounded leaf (*fig. 4*), and the segments of the third order have the frondlike character—even to the circinnate apical growth.

To return to the matter of normal casting of leaflets, with which we began. The fact that in an instance now before us positive evidence of the translocation of absciss-layers, etc., from one part of the leaf to another has been secured, strongly corroborates the inference already made on more speculative grounds, that leaflet-abjection in general is to be understood as an imitative or repetitive phenomenon.

[4] The Whitman fern originated in the greenhouse of H. H. BARROWS & SON, Whitman, Mass., in 1904, as a bud-sport, upon a runner of the Barrows fern (itself a sport from the Pierson).—Letter from H. H. BARROWS & SON to the writer.

The principle of homoeosis

But whether or not the transference of absciss-layer from leaf to leaflets in this fern verifies in any material degree the idea of a translocational origin for leaflet-abjection, it alone, were there no other available demonstration, would suffice to establish the important truth, that a character perfected in the course of evolution under one relation in the plant body may make its appearance suddenly under another relation and in a region of the body to which it is not native. Here is a principle of wide import in morphogenesis, and not without bearing—as has just been shown—upon some of the minor problems of plant evolution; concerning which principle some further observations may be offered.

The described involution of frond-plan belongs to one among several categories of homoeosis all subsumed under the larger type, but of this type it is a rather complicated example. A simpler illustration will make the nature of the general principle clearer, and at the same time exhibit its distinctness from another aspect of morphogenesis with which it is frequently confused—that of reversion.

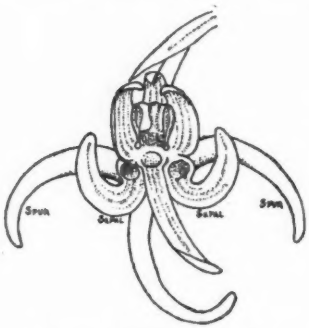

FIG. 5.—Abnormal flower of *Platanthera viridis*, with three spurs. After HEMSLEY.

In 1906 there was discovered in the county of Dorset, in England, a solitary plant of *Platanthera viridis*, the flower of which was remarkable for the possession of three spurs (*fig. 5*), one under the lip in the normal position, and one on each of the lateral sepals.[5] The extraordinary spurs entirely resembled the normal one. The general conformation of the flower was very nearly that of the species, though slight modifications were observable throughout.

The conditions of the occurrence make it highly probable that we have here the offspring of normal parents, rather than one member of a long series of gradually deviating forms; for in a botanically

[5] HEMSLEY, W. B., Journ. Linn. Soc. 38:3. 1907.

often- and well-explored country a race of deviants undergoing a gradual evolution from the typical condition of the species could hardly have escaped observation. It is necessary to suppose that the change of floral structure, in the line of descent embodied in this individual, supervened suddenly. The supernumerary spurs came into existence fully formed. They are not, however, new structures, except when regarded as sepallary appendages, and their origin morphogenetically and historically considered is easily discovered. The spur elaborated and perfected by the usual evolutionary processes—whatever the "usual" processes may be—as an appendage of the lip, has in a moment been transferred in full character to parts which heretofore have not been concerned—namely, to the sepals.

The principle is not new in biology. More than a century ago it began to be observed that when a part of such an animal as a worm is cut off, a new part different from that removed, but like some other part, may grow from the cut surface.[6] BONNET believed that there are special germs for the development of the various organs; as head-germs and tail-germs. From his experiments he made certain inductions concerning the distribution of these germs. LOEB[7] has investigated the conditions under which substitutions for lost parts may be induced, this process being regarded by him as essentially different from regeneration and deserving the distinct name heteromorphosis. LOEB also discovered that in some cases heteromorphosis can be produced without any organ being cut off, or any wound being inflicted upon the animal. Other investigators have dealt with the matter on experimental lines, especially with reference to the physiology of the process. WEISMANN has independently argued the translocation of characters from segment to segment in normal evolution of some insect larvae. He uses the word heterotopia in this connection.[8] BATESON, who appears to have discovered the principle in an original way in his study of variation, gave it the name homoeosis.[9] He describes cases in several phyla; for example,

[6] BONNET, CH., Oeuvres d'histoire naturelle et de philosophie 1:191, 215; 3: 247. 1779.

[7] LOEB, J., Studies in general physiology 115, 191, 627. 1905.

[8] The evolution theory (transl. by THOMPSON) 1:365, 367.

[9] Materials for the study of variation 85. 1894.

in Arthropoda the development of the extremity of a sawfly's antenna in the form of a foot; and in Vertebrata, the not uncommon anomalous presence upon the under side of turbots, etc., of the pigment and the tubercles proper to the upper side.

An interesting case in animals, which has lately come to my notice, is furnished by a crab, the claw being modified as shown in *fig. 6*. The superfluous claw, developed upon the normal dactyl, repeats in detail the style of the larger claw, as regards the general form and even the teeth.[10] The formation is believed not to be congenital, but to result from a wound to the normal claw near the time of moulting.

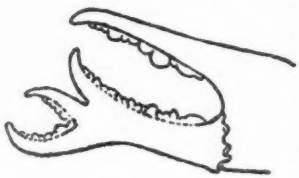

FIG. 6.—Crab claw, showing homoeosis.

The presence of the principle in animal development greatly enhances the interest which the botanical student of morphogenesis must entertain with respect to homoeosis.

In plants the transposition of organs has frequently been described in teratological works; but the phenomena of this class have been confused with those of a different nature, and the larger relations of homoeotic formations have not been recognized by teratologists. MASTERS devotes a short chapter to the subject, under the caption heterotaxy[11]—an expression which, as used by him, seems only in part to cover the ideas I am here endeavoring to formulate. MASTERS' chapter is a miscellany of teratological facts which will not go conveniently into any other chapter of his compendium. His term metamorphy[12] is too general for the present purpose, being employed

[10] Photograph in St. Nicholas Magazine **25**:177. 1907. The specimen is in my possession. A number of similar anomalies have been described by W. FAXON, Bull. Mus. Comp. Zoöl. Harv. Coll. **8**:257. 1881; by F. H. HERRICK in "The American lobster," Bull. U. S. Fish Com. 1895, p. 145, *pl. 47;* and by other writers of whose work a summmary appears in BATESON'S *Materials*. These authors do not specifically recognize the homoeotic nature of the anomaly.

[11] Vegetable teratology 156. 1869.

[12] It will be remembered that GOETHE employed the word metamorphosis in a different sense. SACHS, again, has a definition: "Metamorphosis is the varied development of members of the same morphological significance resulting from their adaptation to definite functions."—SACHS, Text-book of botany, tr. by BENNETT & DYER (1875), 131.

"to distinguish cases where the ordinary course of development has been perverted or changed" (p. 241). This author's *Vegetable teratology*, while it is a rich storehouse of facts for the study of homoeosis, is—as might be expected from the period of its publication—entirely wanting in illuminating discussion and appreciation of relations to the problem of organic evolution such as are to be found in BATESON. The latter author recognizes the presence of homoeosis in plants.[13] SACHS distinguished clearly between atavistic formations and those which are merely translocational. His explanation of the aberrations now being considered would indeed give a degree of literality to the expression *morphic translocation*, since he attributes them to changes in sap movement, with disordered nourishment and abnormal distribution of the formative stuffs.[14] PENZIG'S perception of the real nature of the anomalies now under discussion is clear.[15]

Modes of homoeosis in plants

In the vegetable kingdom homoeosis has many interesting phases, some of which I may indicate. The facts being superabundant, it is well to begin to categorize them, not for mere convenience, but in order that new and possibly suggestive points of view may be won.

1. *The translocation of characters may be acropetal.*

Everyone recalls numerous instances where details of the foliage leaves—toothing, texture, hairing, etc.—have appeared in the floral leaves. A case of acropetal translocation is that of the corolla fringe, peculiar to *Gentiana crinita*, from its normal site to the summit of the carpels.[16] A remarkable transposition has more than once been noted, of the secretory hairs (tentacles) of Drosera foliage to the sepals, petals, and even interior of the carpels.[17]

2. *The transference may be basipetal.*

Petaloid and sepaloid characters—color, texture, outline—not infrequently appear in the involucre, and sometimes the effects reach even the foliage. The most remarkable case that has come to my

[13] BATESON, *op. cit.* 111, 570.

[14] Stoff und Form der Pflanzenorgane, §3. Arbeiten Bot. Inst. Würzburg **2**:452–488. 1882; also Gesam. Abhandl. Planzenphysiologie Bd. **2**:1159–1231. 1893.

[15] Pflanzen-Teratologie **2**:335, 489, etc. 1890–1894.

[16] LEAVITT, Rhodora **7**:14. 1905.

[17] Rhodora, *l. c.*; PLANCHON, Ann. Sci. Nat. Bot. III. **9**:84, 86. *pls. 5, 6.* 1848.

notice occurs in a hybrid of the saffron (*Crocus sativus*). Stigmatic characters in this plant have wandered so far that not only the anthers and floral bracts, but also the foliage leaves are sometimes surmounted by portions of clearly characterized stigma, furnished with papillae; and even the sheaths below the leaves are tinged with saffron color.[18]

3. *Translocation may be lateral.*

Peloria, whether regular or irregular, illustrates this form of homoeosis. In the well-known *Uropedium Lindenii* (*Selenipedium caudatum*, Orchidaceae) the form of the remarkably long pendent petals invades the labellum, entirely subduing the saccate character of that member and converting the strongly zygomorphic into an actinomorphic corolla.[19] Contrariwise, the irregular member may impose its form upon the remainder of the corolla, as in the well-known peloric *Linaria vulgaris*.

4. *The invasion of migrating characters may be partial in any degree.*

The curious modifications of the pistil and its contents in abnormal *Drosera intermedia* illustrate this truth in several different ways.[20] As vegetative influences begin to evince their presence in the flower, the first modification of the gynoecium is an elongation of the ovary, especially its lower part. The carpels, while still concrescent, ovuliferous, and terminated above by the usual stigmatic apparatus, in a slight degree respond to the influx of foreign morphogenetic forces by the lengthening of their basal portions, corresponding to the petioles of foliage leaves: the carpels sensibly approach a petiolate condition. In flowers yet more affected the carpels separate in various degrees, finally falling apart altogether; their bases become elongated to form true petioles; the blades become more and more complanate and spathulate; the ovules after suffering a series of changes are finally replaced by tentacles; and the styles and stigmas, still retained even when the carpel-foliage-leaves spread horizontally from the center of the flower in rosette fashion, lose much of their rightful character. Thus is the gynoecium transformed step by step into a whorl of leaves. The metamorphosis of each part of

[18] CHAPELLIER, P., Journ. Royal Hort. Soc. **24**:277. 1900.

[19] LINDEN, L., Pescat. *pl. 3;* REICHB. F., Xen. Orch. **1**:*pl. 15*.

[20] PLANCHON, *l. c.* 86.

the carpel is marked by the same flexibility and miscibility of characters which pertains to the whole gynoecium. In ovaries affected by the anomaly, but not yet resolved into separate carpellary leaves, ovules become stalked, the integuments may compose a small cup from the edge of which a few tentacles arise, or may be converted into minute modified discoid or concave leaf-blades bearing numerous minute tentacles. Between these blades, representing many characters of the radical leaves of the plant, and apparently perfect ovules, many stages of gradation have been observed. Similarly the stigmas and styles, in the most aberrant carpels, combine with their own characters the structure of marginal tentacles.

The accompanying *fig.* 7 represents advancing petaloid modification of the calyx of *Ranunculus bulbosus*. The normal sepal *A* is green and hairy on the back, while the petal is glabrous and yellow. Sepals *B*, *C*, and *D* are progressively invaded by yellowness and glabrousness (and doubtless by other corolla characters), until in *D* all that remains of sepal nature is hairiness and slight greenness in the median line of the back.

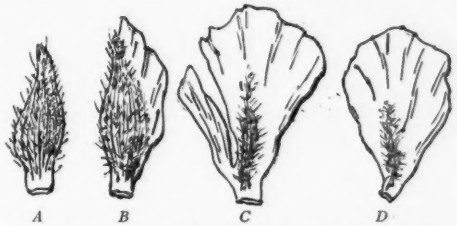

FIG. 7.—Progressive homoeosis in sepals in *Ranunculus bulbosus*. After O. AMES.

The intermediate formations described here, which are of very common occurrence in plants, are the "anamorphoses" of CELAKOVSKY.

5. *Migrating characters may transgress boundaries of homology.*

The term "homologous," applied to organs supposed to have had a common evolutionary origin, is very often vague and not rarely is practically meaningless for the reason that, while degrees of homology are infinite, the specific degree of homology in many cases cannot be known even approximately. In spite of this vagueness in the word, however, most botanists will probably agree that the ovule is in no just sense the homologue of a shoot, nor yet of a pistil, nor of a stamen, nor of a foliage leaf, nor of the droseraceous tentacle. Yet

the fundaments of ovules have been observed to develop into all of these structures. LEITGEB reported[21] a *Marchantia polymorpha* in which cupules of various degrees of development (presumably with gemmae) took exactly the places of archegonia. Yet cupules and archegonia are not homologous.

6. *When against homology, the invasion may be partial in any degree.*

Without entering into details, the literature of ovular abnormality may be cited in support of this opinion.[22] Even when the imitating and imitated structures are known not to be related historically, the presence in any organ of form-giving factors derived from a different organ may merely be indicated by some faint resemblance, or may be pronounced in any degree up to the total replacement of the local member by the foreign.

A corollary of the above propositions (5 and 6) may be stated: Homology of two organs cannot be inferred on the ground alone of the replacement of the one by the other, or of the translocation of features proper to the one into the other of the organs. The existence of even a so-called "complete" series of gradations between two members does not necessarily imply the homology of the members. I think that the anamorphoses of CELAKOVSKY have not the extraordinary phylogenetic significance, as compared with other kinds of abnormality, which this author has attributed to them.

7. *In homoeosis characters may pass from one to the other of the alternating generations.*

YAMANOUCHI has recently published[23] an account of the very interesting conditions attending apogamy in *Nephrodium molle*. The apogamous prothallia bear no functional archegonia, but they proceed to initiate the sporophyte directly. A superficial cell on or near the cushion divides perpendicularly to the surface, and underlying cells divide in various directions. From the complex so originated, the sporophyte develops. The cytological history being followed

[21] Bot. Zeit. 33:747. 1875.

[22] WIGAND, A., Grundlegung des Pflanzen-Teratologie 39. Marburg. 1850; MASTERS, *op. cit.* 186, 262–271; WYDLER, Denkschr. Regensb. Bot. Gesells. 4:77. 1859; PLANCHON, article cited; CELAKOVSKY, Bot. Zeit. 33:129–177. 1875. etc.

[23] BOT. GAZETTE 44:142. 1907; 45:289. 1908.

throughout the critical stages, no nuclear fusions were found; and as a matter of fact the chromosomes of the sporophyte continue to be of the reduced (or x) number. Here we have a sporophytic form imposed homoeotically upon a gametophytic cell basis.

The contrary or aposporic case in ferns has been studied in detail by several workers. In *Athyrium Filix-foemina*, BOWER[24] found the sporangia arrested at various stages, the development being carried on by prothalloid growths which organized typical wedge-shaped cells at one or more points on their margins, while rhizoids were formed at the same time by the outgrowth of individual cells. DRUERY[25] had already observed sex-organs and even young plants arising from these prothallia. WOLLASTON[26] found in *Polystichum angulare* that the tips of pinnules were converted directly into prothallia, bearing archegonia and antheridia. In these cases a gametophytic form is imposed homoeotically upon a sporophytic cell basis (with little doubt; though the cytology, I believe, has yet to be worked out).

Entirely parallel is the production of protonemata from the setae of mosses, as observed by PRINGSHEIM[27] in Hypnum and Bryum, and by STAHL[28] in Ceratodon. LANG[29] has demonstrated the power of Anthoceros capsules to produce thalli aposporically.

The adventive structures are, of course, gametophytic, yet they arise by the prolification of sporophytic tissues.

8. *When the boundary between alternative generations is so transgressed, the invasion of extraneous characters may be partial, and both generations may be represented side by side in the same body.*

GOEBEL[30] has recently induced the formation of prothalloid growths from cut fronds of very young plants in several species of ferns. Some of the aposporous prothallia bore stomata, as well as sex organs (p. 132). LANG[31] found sporangia in various stages of

[24] Journ. Linn. Soc. **21**:360. 1886.

[25] *Ibid.* **21**:354. 1886.

[26] As reported by BOWER, *l. c.* 362.

[27] Monatsb. Akad. Wiss. Berlin, July 10, 1876.

[28] Bot. Zeit. **34**:689. 1876.

[29] Annals of Botany **15**:503. 1901.

[30] Sitzb. Bayer. Akad. Wiss. **37**:119–138. 1907.

[31] Phil. Trans. Roy. Soc. B. **190**:194. 1898.

perfection, produced in groups having a superficial resemblance to sori, upon prothallia of *Scolopendrium vulgare ramulosissimum* which had been growing for a long time without fertilization. LOWE'S cultures of *Scolopendrium vulgare* exhibited the combination of alternative generations in an interesting manner.[32] "We have here consequently a position as nearly as possible intermediate between sporophore and oophore, the sporophoric character distinctly existing in the shape of a circle of stalked fronds generated spirally from a regular axis of growth, while the oophoric character as distinctly appears in the fact that these fronds are practically stalked prothalli bearing the sexual apparatus proper to them."

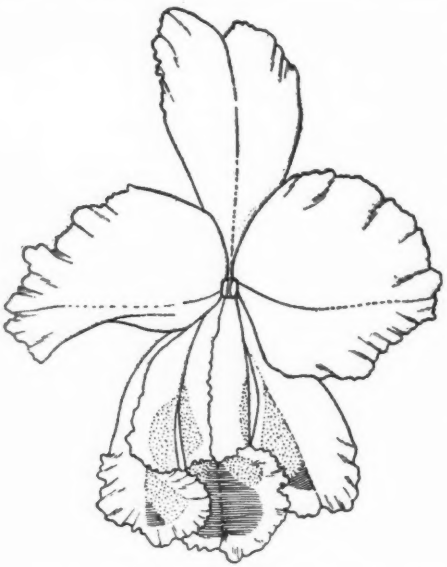

FIG. 8.—Abnormal flower of *Cattleya labiata*. After a colored drawing by O. AMES.

9. *The exact character of a homoeotic metamorphosis is often determined by the nature of the nearest normal organs.*

In many cases proximity appears to be a predominant factor. The following instance conveys more definitely the meaning of this general statement. A plant of *Cattleya labiata*, formerly grown in the greenhouse annexed to this laboratory, produced flowers uniformly exhibiting petaloid homoeosis of the calyx (*fig. 8*). The three sepals—which in normal flowers are rather narrowly lanceolate—were broadened, and their margins were crisped in imitation of the

[32] Journ. Linn. Soc. **32**:536. 1896. The quotation above is from DRUERY'S report in Mr. LOWE'S communication.

ovate crispate petals. The two lateral sepals, however, differed from the dorsal in that the inner half of each became colored like the labellum. The latter organ forms in this species, by the inflection of its margins, a loose tube, embracing the column, open distally and expanding to form the landing-stage for the pollinating insect. The floor of the tube has a broad yellow stripe, widening toward the mouth, and at the extremity replaced by a large purple or crimson-magenta patch. These colors are bounded by the pale magenta body-color of the flower. In the abnormal specimens the halves of the lateral sepals next the labellum reproduced the color-pattern of half the labellum. The halves away from the labellum were like the rest of the flower in hue. This peculiar distribution of the colors becomes interesting when an examination of the base of the perianth shows that in *Cattleya labiata* the foot of each lateral sepal is close to the foot of the labellum and overlaps it by just half—the half corresponding to the homoeotized half-limb in the abnormal flowers; while the other perianth segments stand somewhat apart from the lip. In these particolored sepals the discrimination between homoeotic and non-homoeotic areas seems to be directly related with contiguity to the "source" of the derived features.

PENZIG[33] has dwelt upon this phase of the phenomenon which we are now calling homoeosis, in his general considerations of the significance of monstrosities and in his arguments for the theory of DELPINO regarding the nature of the fertile scale in Abietineae. He was impressed, as everyone must be, with the agreement between the facts of this category and the formative-stuff theory of SACHS.

10. *A compound member may be changed in such a way that some or all of the parts exhibit the plan originally characteristic of the whole member* (*entropic homoeosis*).

The general plan of organization is transferred from the member as a whole to the constituent parts. Compound members may thus, by an entropism of form, suddenly become decompound. This form of homoeosis has already been illustrated in the description of the Pierson fern above. Further examples in leaves of ferns and flowering plants may be noticed here, since this variation has an interesting relation to the question of the evolutionary origin of compounding;

[33] Pflanzen-Teratologie, *l. c.* (and elsewhere).

and besides is interesting from the purely morphogenetic point of view. The same species of variation is also to be observed occasionally in inflorescences.

A glance into two or three private and as many institutional herbaria makes it evident that entropic homoeosis is prevalent in ferns. I have found it in the ten species following, repeatedly in several of them: *Aspidium Thelypteris*, *A. spinulosum*, *Polystichum acrostichoides*, *P. angulare*, *P. Braunii*, *P. munitum*, *Asplenium thelypteroides*, *Dicksonia punctilobula*, *Polypodium vulgare*, *Osmunda cinnamomea*.

Among these species I have found the phenomenon most frequently in *Polystichum* (*Aspidium*) *acrostichoides*, in which species its operation takes some interesting turns. The fronds of *P. acrostichoides* are somewhat dimorphic, not only in the sense of being soriferous and non-soriferous, but also in the fertile and sterile fronds having slightly different general outlines. The sterile fronds have their apical pinnae non-auriculate, obtuse and oblong or elliptical to obovate. In the fertile fronds, the pinnae, again, are dimorphic, the apical ones being shorter, narrower, and abundantly soriferous. Homoeotized pinnae which I have found on various specimens represent the entire range of this dimorphism. A specimen in the herbarium of A. A. EATON, ex-herb. E. J. WINSLOW, collected in Lowman, Chemung Co., N. Y., has the two basal pinnae transformed into miniature fronds. Their length and breadth are increased, and the segmentation is quite perfect. One of them very nearly represents a fertile frond, its terminal portion being constricted and soriferous, and many of the pinnules being auriculate or toothed (*fig. 9*). Some of the pinnules,

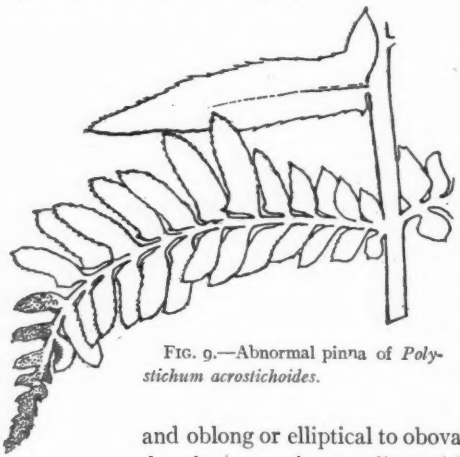

FIG. 9.—Abnormal pinna of *Polystichum acrostichoides*.

however, are of the type found toward the extremity of the infertile frond, as above described. The proximal fourth of this pinna is occupied by pinnules much shorter than the rest, so that the total width of the pinna here is about normal. This region is the part of the pinna corresponding to the stipe of the frond, and would be bare of pinnules were the frond-plan fully realized; as a matter of fact two form-forces are expressed, the pinnar, which gives a blade of proper width on either side of the mid-vein, and the frondescent, which divides the blade. In the opposite basal pinna of this specimen, segmentation is complete, but the homoeosis refers to the terminal pattern of the sterile frond.

FIG. 10.—Normal pinna of *Polystichum Braunii*.

A specimen of this species in the Gray Herbarium marked "Herb. A. GRAY. Near Philadelphia, BOURGUIN," exhibits an interesting interplay of form-factors, wherein that which at first sight appears to be extreme irregularity gradually resolves itself into definite adherence to pre-existing types. Frond-plan in the pinnae is expressed by segmentation and by the character of the segments, by their increased length, and by increased width of the distal two-thirds, and in some of the lower pinnae by the absence of pinnules from the lower side of the pinnar rhachis, throughout the basal one-third or thereabouts of its length—in an "effort" to realize the petiolate condition of a frond. The segments, more or less complete, are those of the apical region of the infertile frond of the species, and the frond-form, in so far as it is realized in the pinnae, is of the infertile type. In these pinnae, the old fashion (pinnar character)

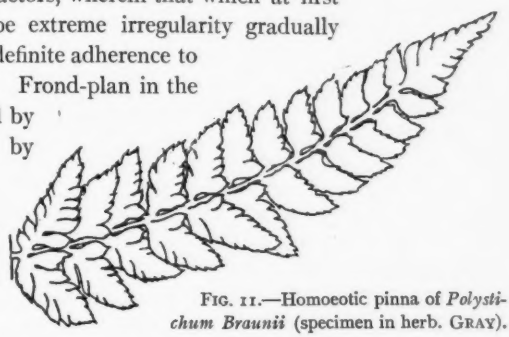

FIG. 11.—Homoeotic pinna of *Polystichum Braunii* (specimen in herb. GRAY).

is able to express itself simultaneously in the morphogenesis, by more or less successfully reducing the segmentation, by maintaining normal width in the basal region of the pinna, and by accentuating the basal segment on the upper side of the pinna, in correspondence with the large tooth or auricle which stands there in normal pinnae. The homoeotic character of the variation is unmistakable, though partial.

In a specimen from the Torrey herbarium, at the New York Botanical Garden, the frondescent pinnae of the lower section of the aberrant frond imitate an occasional trick of the species, by which soriferousness may run down the margin of the sterile region, on the tips of the pinnae. In the Torrey specimen, the lower frondlets (pinnae) are soriferous and constricted in their apical region, and the soriferousness runs down their margins on the tips of the pinnules.

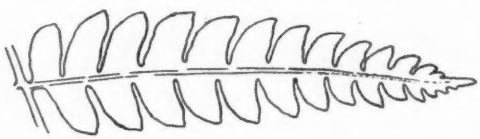

FIG. 12.—Normal pinnule of *Osmunda cinnamomea*.

Dicksonia punctilobula in the herbarium of Mr. F. G. FLOYD shows entropic homoeosis of an interesting type, inasmuch as the

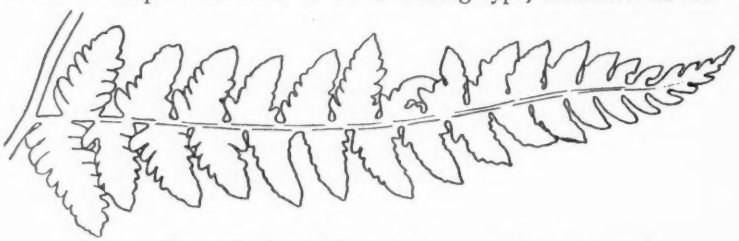

FIG. 13.—Homoeotic pinna in *Osmunda cinnamomea* (in herb. FLOYD).

primary segments become frondescent in imitation, not of the adult but of the infantile, or nepionic, leaves.

Asplenium thelypteroides collected by DAVENPORT and FLOYD at Coon Hollow Brook, Milton, Mass. (hb. FLOYD), has the second and sixth pinnae frondescent (others in a less degree), the modification proceeding upon the basis of the lobing already normally present in

the pinnae, and resulting in the formation of segments of a secondary rank imitating the normal primary segments; and further, in a change in spacing of the divisions, which brings the modified pinnae into conformity with the main frond-plan as regards the distance of the segments. Increased spacing, correlated with perfected divisions, in very obvious homoeosis, is also seen in *Osmunda cinnamomea* (*fig. 13*) collected by F. G. FLOYD at Mt. Desert, Me., where, according to the collector, the form is evidently hereditary, numerous modified plants covering a considerable area.[34]

Coming to flowering plants, the principle is seen in curious variations of the leaves of an Aster which Mr. C. STUART GAGER has kindly shown me. They were briefly noticed by him in *Torreya* for January, 1908. Basal laciniae have become increasingly distinct, some of them even petiolate (petiolulate); and when so, the new, or secondary, blades imitate the main blade, even down to a peculiarity of asymmetrical development.

I regard a leaf condition found by me in *Gleditsia triacanthos* as homoeotic. At any rate the variation noted is very abrupt. The character leaf of the species is simply paripinnate, the leaflets short-stalked, the blade slightly unequal at base, elliptical, obscurely serrulate or crenate, apiculate. In the leaves of vigorous running shoots (not spur shoots) I find some of the leaflets replaced by segments imitating the normal leaf in all the features specified above; the segments are, in effect, character leaves of a second order. The modified, or compound, leaflets, which are nearly twice as long as the unmodified ones, occur irregularly among the others (*fig. 14*). The condition here, essentially the same as that described for the Pierson fern, has been noticed also by GAGER (*l. c.*), one of his specimens—as also one of mine—carrying the homoeosis to the second degree, a few *pinnules* becoming perfectly compounded (as in the Whitman fern). There is no evidence, so far as I know, that the modified condition looks back to an older, normal state of division. What happens is that segments of the leaf are transformed into the likeness of something now existing—the normal, or character, leaf of

[34] Examples of entropic homoeosis may be found in MOORE and LINDLEY, The ferns of Great Britain, etc., Nature printed. London. 1857; and in MOORE, Nature printed British ferns. London. 1859 (?).

the species. The likeness is perfect. Whether the variation here is admitted to be at the present time in each instance a fresh display of homoeosis, or is suspected of being reversionary, the abruptness of the change and the manner of its occurrence seem to me plain indications of the origin of the decompounding. It seems to me far more likely that this is entropic homoeosis, past or present, than that the complex form of the compound segments was worked into perfect likeness to the original blade slowly by natural selection.

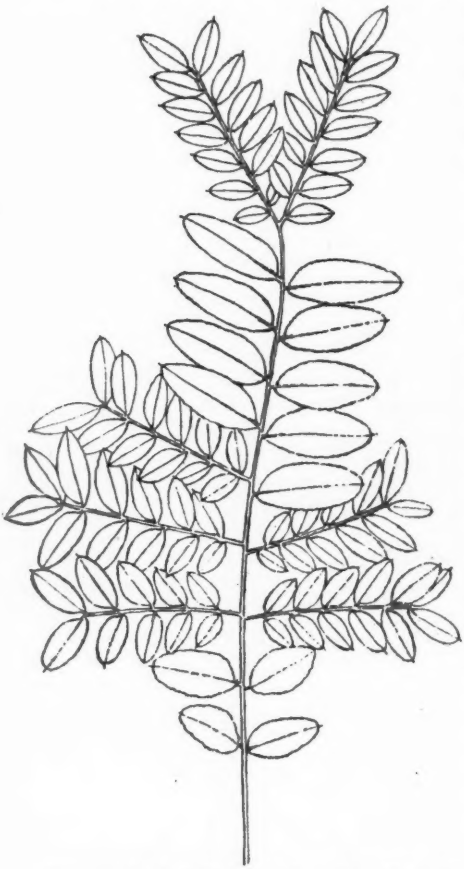

FIG. 14.—Leaf of *Gleditsia triacanthos* with seven homoeotic pinnae.

BONNET recorded a variation of the jasmine (*Jasminum officinale*) which is seen to be homoeotic in a similar way. *Fig. 15* shows the normal and variant forms side by side, as delineated by BONNET (Oeuvres **2**:363. *pl. 24*).

Inflorescences of certain marked types sometimes undergo entropic homoeosis; for example, umbels and pseudumbels. Of the former I have seen two cases, the first in *Aralia nudicaulis* (specimen in hb. N. Y. Bot. Garden, coll. by AUSTIN C. APGAR, near Lambertville, N. J., 1887). This species normally bears simple umbels at the ends

of the three main branches of the scape. In APGAR'S specimen some of the florets in each umbel are replaced by long-pedicelled umbellules. That is, the form resident in the flower cluster as a whole has instantly passed into several of the parts (florets). A similar variation I have seen in *Hydrocotyle umbellata* (specimen in hb. N. Y. Bot. Garden, Jamaica, FERRY, no. 6168): and in *Daucus Carota* it was noted by CRAMER,[35] radial florets being replaced by umbels.

FIG. 15.—Normal leaf of jasmine (left) and a leaf with homoeotic segments (right). After BONNET.

Two false umbels of Pelargonium in my possession are abnormal in a similar way. In each case one of the florets, eccentrically situated, has been transformed homoeotically, with the result that it rises as a pseudumbel of a secondary order from amid the flowers of the first. The subordinate flower cluster is like the chief cluster as regards centrifugal development, involucre, etc., though the flowers are fewer (8 instead of 18) and shorter-pedicelled. The secondary peduncle is articulated to the expanded summit of the primary, as are the pedicels of the flowers, and apparently would have been cast off, in event of failure to fertilize, by an abscis-layer, as with the flowers among which it stands.

Homoeosis and reversion

I have said that homoeosis is often confused with reversion; indeed among botanists the confusion may be said to have been habitual. The older writers having applied to homoeotic phenomena the word reversion in its ancient sense, some contemporary authors have with little reflection retained the antiquated language in expressing ideas which are altogether modern.[36]

[35] CRAMER, C., Bildungsabweichungen bei einigen wichtigeren Pflanzenfam., etc. 63. Zurich. 1864.

[36] In Rhodora 7:18, 19. 1905, I have discussed briefly the origin and use of the reversion idea as applied to plants.

In order that the real relations of the forms concerned shall be more generally recognized, one needs but to direct attention to them; argument is scarcely needed. For example, the appearance of two supernumerary spurs in *Platanthera viridis* is palpably anything but atavistic. No one at all conversant with Orchidaceae will for a moment imagine that there ever was an ancestral race of three-spurred Habenarias to which the curious Dorset plant harks back. In the above-mentioned gentian with the fringed carpel, the relation of things in evolutionary time is perfectly clear. While the carpel is an ancient, the fringe is a very recent, structure; the former was not derived from a petal, and the fringe has never until now been a carpellary appendage. When the carpel puts on the fringe, therefore, it adopts a character not to be found in its own phylogenetic line. Simply the fringe is borrowed; there is no reversion. The non-atavistic nature of the stigmatic papillae on bracts and foliage of *Crocus sativus* is equally patent. The assumption of foliage characters by carpels of Drosera is no more reversionary. The carpel of Drosera, it is safe to say, had its origin in common with that of other angiosperms, and runs back through a series of forms, none of which is a foliage leaf, to the megasporophyll of the earliest angiospermous seed-plants. Likewise the foliage leaf of Drosera is a derived structure, with characters probably more recent than the family Droseraceae even. Its peculiarities of contour and its appendages arose long subsequently to the establishment of the angiospermous, and even the droseraceous, carpel. To reach a point whence these two lines of derivation diverged, i. e., a point where the reproductive and the vegetative organs were one and the same member of the plant body, we must probably go back to the spore-bearing foliage leaf of the fernlike ancestry, far antedating the first flowering plants. The common original of the Drosera carpel and the Drosera foliage leaf was probably a kind of fern frond. The aberrant carpels in question bear no resemblance to fern fronds. They do not reproduce a form from which they are descended. They have simply taken to themselves properties of coordinate derivative members, the foliage leaves. This is so obvious that the statement would seem superflous were it not still the custom of inconsiderate writers to speak of such metamorphoses as reversions in the phylogenetic sense. The transforma-

tion is not retrograde in any except an imaginary sense; since the normal unmodified carpel is to be regarded as already "retrograde," or conservative, as compared with the tentaculiferous leaf; and the ovule as vastly more ancient than the tentacle into which it suffers change.

In peloria the morphogenetic relations are not so instantly obvious. However, the phenomenon is usually, if not always, better viewed as a homoeotic, than as an atavistic, occurrence. In notices of peloric monstrosities one often meets with the statement that these formations have a historical value. Thus, with respect to a peloric Laelio-Cattleya, MASTERS[37] suggests that here is a reversion to the earlier and simpler conformation from which the peculiar orchid structure, as we know it, has evolved. While this is true abstractly, in a merely descriptive sense—since actinomorphy doubtless preceded zygomorphy in the monocotyledonous phylum—yet it is probably untrue if we are to take it in any real phylogenetic sense, with the understanding that actinomorphy has remained latent as a hereditary character through the enormously long period of the evolution of this family from an actinomorphic condition. Regular peloria is to be considered in conjunction with the opposite change, which frequently occurs in orchids. The antithesis of the two pelorias makes it evident that we have here something besides atavism; since if either form is atavistic the other cannot be. This outcome, coupled with the fact that we have a less objectionable construction, discredits the entire idea of reversion in peloric orchids. The argument extends to other families.

Without further expatiation, it will be evident—if the standpoint of the present paper is correct—that the word reversion is a much-abused term. True reversions, except those which occur periodically in the ontogenesis, are, I suspect, rather rare. Atavism is never to be assumed off-hand in teratological cases, but it is to be admitted only when established by aid of independent proof. It should be borne in mind that *antecedents of monstrous forms are much more often to be sought in contemporary normal parts than in ancestral conditions.*

The place of these facts in botanical theory

The facts to which I am referring from a special point of view have values in botanical theory in at least three different relations:

[37] Gard. Chron. II. **31**:235, 239. 1902.

first, a study of the modes or phases of homoeosis helps us to estimate at its true worth teratological evidence applied to the solution of phylogenetic problems; *secondly*, the facts seem to throw light on the method of evolution of some normal structures; *thirdly* and chiefly, the facts of homoeosis constitute, as has been already pointed out in the introductory passage, an important section of the data of morphogenetics. Let us examine these relations of the subject a little more in detail.

1. The study of homoeosis must somewhat increase the caution with which we use deviations from the normal as aids to morphological interpretation.

In the past the commonest use of abnormalities has been to make them the ground of phylogenetic inductions. The stereotyped remark of writers describing monstrous specimens has been that such aberrations "are very instructive"—an expression of faith either in the phylogenetically reversionary nature of abnormalities, or in the eternal inviolability of homology in morphogenetic sequences. Surmises from monstrosity alone were naturally more common in the days when the evolutionary story of plants was less complete than it is now, and when morphologists were driven to indirect and speculative methods. The history of this subject is voluminous; perhaps, though interesting as a study in speculation, it is more valuable for the errors which it embodies than for any content of truth; and it will not be entered into here. Some of the contentions for which teratological formations were used have been abandoned, and others have been settled by the discovery of direct evidence from comparative morphological studies of living and extinct plants. As we are enabled by extension of knowledge and maturing of opinion to understand better the relations of both normal and abnormal forms, it becomes evident that the imagined morphological significance of many abnormalities falls to *nil*. For example, we now know that the conversion of the nucellus of an ovule to a shoot, as in Aliaria and in Drosera, is wholly without phylogenetic meaning. From a study of even normal organization we are losing the belief of earlier botanists in the absolute integrity of morphological categories; and if the observations assembled in the present essay are accepted in

the sense in which they are presented, it is indisputable that stages of development supposed to be concatennated in a fixed order are subject to the most violent dislocation—that a stage belonging to one morphological category may pass into another of a different category.

Abnormalities which are traceable to very ordinary features of contemporaneous organization and may be brought under the rule of homoeosis, will for the moment lose all historical force which they may ever have been thought to possess. Historical significance can be restored to them only by application of the laws (if we may so speak of the operations) of homoeosis. If homoeosis much more easily follows lines of homology, and only rarely transgresses them under very special conditions, then frequent homoeotic metamorphosis of a particular organ in a particular direction may be thought to be indicative of the derivation of the organ. But I think that the admission of homoeosis in any case is practically fatal. The method of inference then becomes too roundabout to be acceptable to modern taste. If in any case homoeotic formations agree with the results of comparative morphology, of anatomy, and of organogeny, still they add only a reflected light to the general illumination.

In writing these words I have in mind particularly the long debate over the morphological nature, or origin, of the ovuliferous scale in conifers; or so much of it as relates to malformations. Perhaps no single organ of vascular plants has afforded morphologists more matter for disputation than this scale, which has a vast literature of its own by the most eminent authorities—LINNAEUS, A. BRAUN, SCHLEIDEN, VON MOHL, EICHLER, SACHS, BAILLON, STRASBURGER, VAN TIEGHEM, DELPINO, PENZIG, MASTERS, NOLL, CELAKOVSKY, and others. The theories of these authors have been various, and based upon every conceivable consideration, not least upon abnormalities. Teratology has appealed very differently to different students—to some as supporting one doctrine, to others as favoring a different theory; to some as of great or even decisive weight, to others as having no significance at all. CELAKOVSKY, who has studied the matter most persistently, has relied upon abnormalities, and especially upon unbroken series of intermediate formations, such as those between the fertile scale as it separates into parts (at the appearance of a shoot) and the leaves (or bud scales) of the shoot. This

author assumes that such gradations can exist only between homologous organs. He regards the entire composite structures found in the monstrous cones, made up of the fertile scales and the shoots which grow through them, as such intermediate formations (anamorphoses), and looks upon them as sufficiently proving the shoot-nature of the fertile scale.[38]

From the numerous clear and detailed drawings of the abnormal cones which have been published,[39] certain truths are apparent enough. First, no new organ or form of any organ, not proper to the species of today, except intermediate formations between present-day vegetative and reproductive parts, is to be found in the cones. No ancient structure, nor anything suggesting ancestral structures, nor any organ of paleobotanical aspect, makes its reappearance out of the past; there is no reversion. If the shoot in the axil of the bract, replacing the scale, were truly atavistic, we should expect that lost characters would appear in the axis and its appendages. But the shoot turns out always to be an ordinary leafy branch with the reduced foliage representing the xerophytic adaptation of the group. This shoot is not reversionary in even a barren formal and descriptive sense; for if the fertile scale represents a shoot, now reduced to two ovules and their expanded integuments, the relics of two sporophylls, and if the original development of axis and sporophylls is to be restored, we ought to have in the restoration an axis terminated by sporophylls or by ovules as representing them, since megasporophylls when reduced to a pair are terminal appendages; but this development is not realized in the abnormal cones, in which we find that the shoot arises sometimes above or below the scale, and when in the midst of it, then in the form, not of a stalk, but of a proliferation, upon which the parts of the fertile scale become basal appendages—if they are to be taken as appendages of this shoot at all.

The transformations of the cone are homoeotic. And therefore,

[38] CELAKOVSKY's writings summarize the whole controversy (Abh. Kgl. Böhm. Gesell. Wiss. VI. **11**:1882; VII. **4**:1892; ENGLER's Bot. Jahrb. **24**:202. 1898). More accessible may be WORSDELL's review (Annals of Botany **14**:39. 1900), or that of COULTER and CHAMBERLAIN (Gymnosperms 69–77. 1901).

[39] E. g., CELAKOVSKY, Abh. Kgl. Böhm. Gesell. VI. **11**:1882; PARLATORE, Ann Sci. Bot. IV. **16**:*pl. 13*. 1862; STENZEL, Nov. Act. Nat. Cur. **38**:*pls. 12–15*. 1876; VELENOVSKY, Flora **71**:*pl. 11*. 1888.

while it is in itself not unlikely that the fertile scale represents a pair of sporophylls belonging to an axillary shoot, and while comparative morphology and anatomy may make this view even probable, the monstrous cones, it seems to me, add nothing material to the satisfaction which one may take in this solution of the conundrum.

Nor is their value improved by the anamorphosis idea. To me at least the "transitions" from fertile scale to axillary shoot do not appeal with the same compulsion with which they appeal to CELAKOVSKY and some others. I can conceive the most perfect of these transitions to represent combinations of historically unrelated form-factors, reproductive on the one hand and vegetative on the other; and in the conception I find nothing incongruous with other facts of homoeosis. If there were originally no shoot in the axil of the fertile leaf (the bract) but only an ovuliferous segment (SACHS-EICHLER) or pair of lobes (DELPINO)—supposing for argument that these notions were admissible on any but teratological evidence—and if by influx of vegetative forces the cone were converted *gradatim* into an ordinary branch, with buds in the axils of the leaves; then it seems to me that we might expect to discover morphogenetic impulses toward the formation of ovuliferous segments and impulses toward bud-formation coexistent and cooperative in the same body of axillary tissue, with such a result as the monstrous cones exhibit. After reviewing the combinations of diverse formative impulses in teratological occurrences generally, I do not feel that CELAKOVSKY'S case for the pre-eminent value of anamorphoses is established. In comparison with other sources of suggestion the monstrous cones seem to have a minimal value. The interest and worth of CELAKOVSKY'S thoroughgoing study of the whole subject does not lie in his treatment of monstrosities.

Yet a small degree of approval for the theory which makes the scale represent a shoot bearing sporophylls might possibly be derived from the frequency with which a shoot arises in the site of the scale; and this in spite of the facts that there are irregularities and that more than one plausible reason might be given for the frequent appearance of the shoot. The latter has been found in the genera Larix, Picea, Pinus, Tsuga, Cryptomeria, Cunninghamia, Glyptostrobus, Sequoia, Taxodium, and some other genera.

I hope that it may be clear that the shoot-and-sporophyll theory is not here called in question, but only the use of teratological formations as competent evidence. The ground is taken that these formations do not remove all doubt as to the origin of the fertile scale, but on the contrary only after all doubt has been removed as to the nature of the scale, by legitimate argument from comparison of normal structures, do the monstrous formations begin to have any considerable historical significance.

2. Homoeosis has played a part—necessarily from its nature, which is essentially anarchical, a small part—in the evolution of plants. We can trace to a homoeotic origin certain established sequences in development, of which specific examples may be adduced.

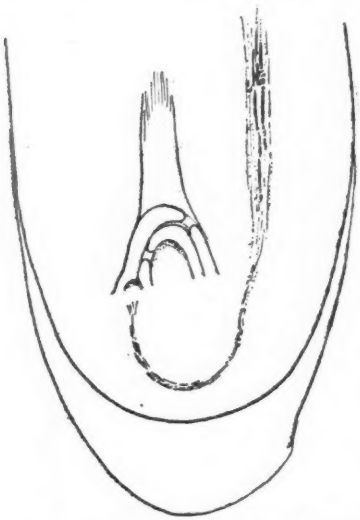

FIG. 16.—Median longitudinal section of root of *Habenaria quinqueseta*.

(*a*) *Habenaria quinqueseta* (or *Michauxii*) of the southern states carries on vegetative reproduction by certain of its roots. At the apex of these roots, close to the *punctum vegetationis*, pointing backward in the embryonic tissues, a stem apex is organized. *Fig. 16* shows its relations to the apical regions of the root. Two leaves and a bud in the axil of one of them have already been differentiated. Subsequently to the stage here represented, the root-apex enlarges and forms at the base of the new shoot a spherical tuberoid growth evidently with storage functions.

As to the evolution of a shoot fundament in this curious position, no one, I suppose, will imagine that the entire evolutionary history of the stem, leaf, and bud in cormophytes has been repeated in the

interior of a Habenaria root. It is perfectly clear that the form-giving agencies which shape the leafy shoot in this species have been set to work upon tissues which up to a certain point have been dominated by other forces. There is nothing new except the extraordinary morphogenetic sequence. In this instance, morphic translocation has become habitual, or normal.

(*b*) In *Phyllonoma ruscifolia* of Mexico the flowers are regularly produced from the upper surface of leaves, near the apex (*fig. 17*). There is no adnation in this case, for the anatomy of the blade below the inflorescence and of the petiole shows no addition to the normal vascular structure, indicating any concrescence. Here again an abrogation of ordinary morphogenetic sequence has become fixed in the development.

FIG. 17.—Leaf of *Phyllonoma ruscifolia.*

(*c*) The specific form of the vegetatively derived embryo in some plants must be considered homoeotic; as for example in *Opuntia vulgaris*, described and figured by GANONG.[40] At the time when fertilization should take place, the egg cell, according to GANONG'S observation, has become disorganized. The place of the normal embryo is taken by several embryos budding in from the nucellus. The noteworthy feature of these apogamous individuals is their adoption of the form of the abdicating embryo proper. Here is a homoeosis which has become established and provides a regular means of propagation for the species. A considerable number of such cases is known.

It is natural to imagine that conditions in the embryo sac determine the form of the buds and cause the homoeosis; yet it is not at all certain that such is the explanation of the assumption of form. In a case observed by myself the embryos organize outside of the sac. I refer to *Spiranthes cernua* of the meadows. The upland form of the species has a normal development. In the variety growing everywhere in rich meadows I have seen only polyembryonic seed. Having followed the development with care, I find that the

[40] BOT. GAZETTE **25**:221. 1898.

embryo sac ceases to develop after a few nuclei have been formed in it, and is pushed aside by the hypertrophic inner integument. This envelope, normally composed of a few flattened cells overlying the sac, in this variety of the species early takes on a very active growth, forming a mass of cells which, as it comes to maturity, splits up into rounded bodies simulating the embryo of the genus.[41] The formation of embryos is often incomplete and growth then results in amorphous masses; but on the other hand, it is often successful, and gives such seed-contents, consisting of several well-made embryos, as that figured herewith (*fig. 18*). It is true that the form is very simple, for the normal embryo has neither suspensor nor cotyledons. But that cells of the inner integument, ordinarily forming a saccate one-celled layer, with not the remotest resemblance to an embryo, should so much change their habits, and in the transformation should select the fashion, though simple, of embryos, is sufficiently singular. I look upon the process as homoeotic in its nature.

FIG. 18.—Seed of *Spiranthes cernua* (lowland form).

The formation of embryos here is quite independent of pollination, as I have proved by carefully castrated and guarded flowers—an ecologically important item for a species blooming so late in the season. The biological significance of the process, indeed, is—if I may digress for a moment—that the plant by this means combines the certainty of issue which pertains to vegetative methods of reproduction, with the swiftness of dispersal and range of dissemination secured by the seed apparatus. This is doubtless the combination of favorable circumstances which has secured the wide adoption of apogamy in Compositae also. In *Spiranthes cernua*, homoeosis supervening in the integument has doubtless contributed to the abundance of the species in suitable soils from Massachusetts and Ontario to Georgia (I know not how much beyond these limits, which bound my search for the polyembryonic condition).

(*d*) Still more remarkable is the transference, discovered by

[41] Rhodora 2:227. 1900.

ROSENBERG,[42] of a whole series of characters from the megaspore and embryo sac to a somatic cell in *Hieracium flagellare*. The embryo sac is sometimes formed normally, but in the greatest number of cases this structure aborts. A neighboring cell, which may be situated in the epidermis of the nucellus or in the chalazal region or in the integument, takes upon itself the function of a megaspore, though without reduction of the chromosome number. This cell enlarges to form an embryo sac. Its nucleus divides as that of the megaspore would do; egg apparatus and antipodals are formed; and even polar nuclei fuse to form an endosperm nucleus. The gametophyte is thus reproduced, after the failure of the proper organ to construct it, by a cell of the sporophytic generation. And this homoeotic process is habitual, hereditary, and established in the species.

If HEGELMAIER'S observations upon *Lycopodium Selago* are correct,[43] we may attribute the formation of the gemmae of this species and its near allies to a homoeotic origin. The gemmae—detachable shoots—arise in exactly the position of leaves, from which in their earliest stages they are indistinguishable.

The form of homoeosis most often entering into the diversification of species of plants is apparently that which has above been called entropic. Abscission of leaflets has already been discussed in this connection. Another seemingly homoeotic feature of compound leaves is found in their stipels. An examination of stipels in a considerable number of groups—as in Xanthoxylum, Staphylea, Enscaphis, Turpinia, Robinia, Bradburya, Desmodium, Galactia, Dolicholus, Vigna, Amorpha, Sambucus—strongly suggests that the stipels have arisen as echoes of the antecedent structures, stipules, when in the evolution of the leaf suitable conditions have been established. They occur in plants possessing stipules, and with little doubt already in possession of them before leaf-compounding set in; they are generally useless, as far as one can see; when they have a visible use it is the same as that of the stipules, in a much weakened degree; they follow punctiliously the greatly vary-

[42] Bot. Tidsskrift **28**:150. 1907.

[43] Bot. Zeit. **30**:841. 1872.

ing character of the stipules—being large, stout, and thorny; slender, terete, rigid, and sharp-pointed; long, weak, and membranaceous; small or evanescent or flattened and glandular-capitate, etc.—in the different groups; they occur in situations much resembling the situations occupied by the stipules. All of these facts suggest that the compounding of the leaf with organization of partial leaf-stalks, in evolution, has been the occasion for the production of stipels homoeotically.

Moreover, we may well suspect that in many cases decompounding of the blade has followed upon compounding from the same general cause; the partial blades borrowing the compounding tendency from the parent blade, the whole leaf thus becoming by a single step decompound. The circumstance that the ground-plan of the whole leaf is repeated in miniature in the several parts, in a vast number of decompound leaves of both phanerogams and ferns, and the occurrence of the corresponding type of homoeosis as individual variation in both divisions, lend a color of probability to this conception. Decompounding, on this hypothesis, would have no initial relation to utility, and would not be a product of natural selection.

To consider this matter a little further with respect to ferns: If the variation which we find so frequently in ferns has been the basis of evolutionary advance in complexity of the frond, we should be able to discover in the decompound-leaved species certain relations which would necessarily follow from such an evolution. We should certainly find the ground-plan repeated in the segments. We should expect to find, further, that the historically earlier and simpler conditions would be retained in youthful leaves; and that these youthful leaves would be matched by the segments of the fully developed fronds of the mature plant. Both these expectations are met in many species. Ferns on every hand illustrate the first. Of the second, a single example will be enough to direct attention to the facts which are easily observable. In *fig. 19* are reproduced a youthful frond of *Polystichum angulare proliferum*, and a pinna from an adult leaf. In *Asplenium Filix-foemina* we have a depauperate variety, var. *exile* D. C. Eaton, the mature frond of which is very precisely matched by the pinna of the frond of the typical form.[44]

[44] See EATON'S Ferns of North America *pl. 76*.

Further, if entropic homoeosis has given us decompounding widely in ferns, we shall expect to find species so related to each other that some represent the original types and others the homoeotic derivatives. We shall look for, first, the simply pinnate types; secondly, types in which the pinnae match the fronds of type *1;* and perhaps thirdly, a type in which the fundamental plan is worked out in the pinnules. If the simple type has two modes, as above described for *Polystichum acrostichoides*, we may expect to find either or both represented in the more complex patterns.

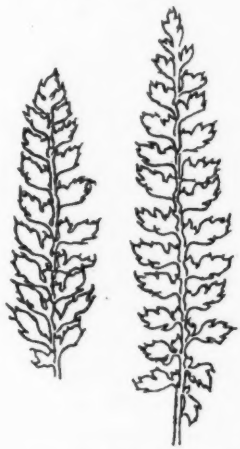

FIG. 19.—Youthful frond and pinna from adult frond of *Polystichum angulare proliferum.*

Anyone having access to a collection of Polystichum may see this projected scheme filled out by existent species. First we have the simply pinnate forms, such as *P. acrostichoides*, *P. munitum*, *P. lonchitis;* in which we have two frond patterns, *1a* being the fashion with more or less oblong, non-auriculate pinnae, probably historically earlier, seen in a pical regions of sterile fronds; and *2b* being the characteristic plan, the pinnae falcate-auriculate. Then we find many species with pinnae frondescent in facsimile of pattern *1a* or *1b;* as *P. californicum* (*1a*) and *P. Lemmonii* (*1a*), *P. aculeatum* (*1b*), and *P. Braunii* (*fig. 10*, *1b*, sometimes *1a*); and others, a considerable number of species. Finally, frondescence of the second degree is well represented in *P. angulare tripinnatum* (*1a*, in the ultimate segments). In *P. scopulinum* the (supposititious) homoeosis is incomplete, the proximal region of the pinnae alone being segmented (*1a*), the distal merely lobed.

We find species so much alike (except that one of two is simply pinnate, the other decompound) that one appears to have been derived directly from the other by entropic homoeosis; as the West Indian *P. viviparum* (decompound *1a*) from *P. triangulum* (compound). In Europe *P. aculeatum* and *P. lonchitis* stand in a similar

relation to each other; the slight differences—apart from homoeosis—are such as might be expected to arise in specific isolation.

In homoeosis a character or a system of organization which has been evolved in one part of the body is transferred, ready made, to another part. The great mass of instances are of the class called teratological. By this designation we mean, substantially, that they are suddenly appearing deviations from the customary structure. "Monstrosities" in general have the special value that their chronology is oftentimes ascertainable; we know that such and such identical plants have arisen in the midst of normal relatives. They exhibit, as has been said, discontinuous or saltatory variation. That homoeotic monstrosities typify homoeosis in general, as a saltation phenomenon, may be inferred from the very nature of the process. When, therefore, we discover homoeosis at work in normal evolution, diversifying lines of descent, we are able to augment the steadily increasing collection of evidences for discontinuity in the origin of specific differences.

Homoeotic changes may thus be classed with mutational phenomena. But grouping them with the mutations exhibited by the Oenotheras rests only upon some such negative property as that homoeotic transformations fall outside of any law of the evolution of characters by natural selection. It seems unlikely that the two classes of alterations have anything further in common. Mutation proper seems to result from some qualitative change in the inheritable substratum of organization; while in homoeosis no new qualities are introduced, but only old characters are recombined, or characters are evoked in a new sequence in development. Homoeotic transformations are, indeed, found among the instances of mutation which DE VRIES uses in *Die Mutationstheorie* (for example, peloric *Linaria vulgaris*). They have to be classified under this author's *degressive Artbildung* (p. 461, B 2, a). Yet their inclusion in a classificatory scheme of variations under mutation seems to rest on purely formal and abstract descriptive resemblances.

3. The idea of homoeosis unites for descriptive purposes a great number of facts of ontogenesis which, even though they may not

at the present juncture point a way to the correct mechanical explanation of development, possess in this connection a considerable prospective value. An adequate theory of ontogenesis must take these facts into account.

Their value lies in their exceptionality. Homoeotic occurrences are fundamentally antithetic to our usual conception of the method of development. The most general and fundamental of our notions of a mechanically autonomic evolution from egg to adult, is that of a series of states (A, B, C, D . . . . X, Y, Z), so related that each one necessarily serves as the stage upon which the next state arises. Every one of the several states seems to be the needful condition for the appearance of the next following. This is the primary conception of ontogenesis derived from ordinary experience. It is contradicted by homoeotic formations. We see the usual sequence violated at some point, and a state (as X) arising upon a state (as D) from which it does not normally arise, and from which we have supposed that, in the very nature of the process, it cannot arise directly.

In homoeosis, then, we have a new ontogenetic phenomenon. Herein lies its worth; for every datum of a new sort adds to the materials for a true theory of development, and increases the chances of our finding a clew to the right construction and combination of the materials.

Although the times are doubtless not ripe for the appearance of an adequate theory, and further attempts in this direction may be profitless for the present, yet almost universally there has been felt the desirability of biomechanical hypotheses going behind the bare facts of development. We have had from DARWIN, NÄGELI, DEVRIES, SACHS, ROUX, WEISMANN, DRIESCH, and others a series of more or less elaborate attempts at an explanation. I think that anyone at all familiar with this line of biologic endeavor will recognize the progress in substantial knowledge effected under the influence of such speculations—even though they deal with gemmules, pangens, micellae, biophores, and less concrete "organizations," far beyond the range of the microscope. And it is entirely possible that some of the suggestions already offered may be germinal points from which a verifiable system will develop.

The most persistent attempt at a solution has been made by WEIS-

MANN, who has erected a theory of the nucleocentric type, wherein the control of development is made to reside within the several cells, and specifically within the chromatic matters of the nucleus. Nuclear divisions are conceived as being of two types; namely, (1) equating, in which the germ-plasm is conserved in its integrity, all characters of the mother nucleus being shared equally by the daughter nuclei; and (2) differentiating division, in which the daughter nuclei receive from the parent nucleus unlike assortments of character-giving bodies. All the determinants, capable of giving form to the whole organism, being present in the nucleus of the egg, differentiation is concomitant with an orderly distribution of the governing bodies, effected in the successive nuclear divisions, each different part of the body ultimately receiving its proper kind of determinant.

In view of present limitations of our knowledge, the theory of WEISMANN is a highly speculative system, and as such has been freely modified to meet emergencies arising from the discovery of new facts. There is perhaps little forensic satisfaction to be gained from argument under these conditions. Yet it is undoubted that the the proposal of this hypothesis has prompted investigations leading to interesting discoveries. And even as a means of throwing observations into some sort of order, any such theoretic scheme has its use. It seems to me, therefore, well worth while to consider all kinds of facts of ontogenesis in the light of this and other generalizations in morphogenetics. The facts of regeneration have thus been arrayed with relation to the Roux-Weismann hypothesis. Regenerative phenomena take on, in consequence, some new aspects, and the whole subject gains in spirit. A tentative relation is established between regeneration and morphogenetical theory in general.

The effect upon the Roux-Weismann theory has been the introduction of a fundamental modification. For the power of reproducing lost parts, so widely possessed by animals, and in some degree by plants, is not accounted for by the Roux-Weismann idea in its most unequivocal form. To allow for this faculty, the cells, even of differentiated tissues, instead of being deprived of all elements except those expressed in the usual form of these tissues, are now allowed to retain sets of determinants sufficient for purposes of regeneration. This auxiliary equipment is, however, tightly stowed. Under ordi-

nary conditions only the *differential* determinants are free to influence the development of the cell and its activities, the regenerative or reserve determinants being held strictly under restraint until they are called for, to reconstruct lost members.

Homoeosis has a similar influence with regeneration upon the Roux-Weismann idea; and perhaps a more destructive influence. For while the facts are quite as striking, they are very much more varied and abundant. And if the vast array of data, the existence of which has been suggested in the present article, is added to the evidence from regeneration, the necessity for providing full reserve-funds of determinants in differentiated parts is much increased. Many parts of the body—this statement is made especially with reference to plants—are able to produce almost any other part. We are probably warranted in postulating a pangenerative capacity for every vital member. We know that a single epidermal cell of the leaf in Begonia may originate a complete plant. Indications are not wanting that single living plant cells in general intrinsically possess the same power, ordinarily latent, its exercise inhibited by circumstances. If each cell possesses a complete character-fund, the characters capable of being severally activated upon motion of factors external to the cell, does not the necessity for imaging special individualized determinants disappear? Can we not as well think that differences in cells and forms of organs spring from the nature of the molecule of the form-giving substance (probably chromatin), this substance being the seat of morphogenetic powers ready to be evoked and responding variously to the diverse conditions in which, in the course of development, the substance finds itself placed? Obviously, in proportion as all cells of an organism are made to appear equipotential in a morphogenetic sense, does the need of assuming the existence of different kinds of form-giving substance diminish.

Whatever be the basis assumed for an explanation of the microevolution which we call ontogenesis—whether the existence of special form-controlling bodies, or the general properties of the organic molecules, or organ-forming stuffs capable of diffusion, or some other basis—the abrupt diversion of formative currents and transformation of members into others of usually dissimilar origin, the frequent appearance of forms in locations not expected in the ordi-

nary sequence of development, and the potentiality of all parts in each part, indicated by the general phenomenon which we have been calling homoeosis, will need to be provided for in our ultimate theory of development.

STATE NORMAL SCHOOL
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BRIEFER ARTICLES

LONGEVITY OF SEEDS

In a recent article on longevity of seeds, EWART[1] makes a number of statements which merit comment. He assumes as correct the claim of BERGTHEIL and DAY[2] (working on *Indigofera arrecta*) that they have priority in discovering that the water-resisting power of the seeds of legumes is due to the character of an outer layer of the coat. NOBBE,[3] however, pointed out the fact for *Trifolium pratense* 31 years before the publication by BERGTHEIL and DAY. Both find that stains dissolved in water penetrate in the hard seeds only through the very thin outer layer, called cuticle by NOBBE; but that they do not pass through the palisade layer. This is shown in *fig. 1* of BERGTHEIL and DAY's article. EWART finds the resistance in *Adansonia digitata* to be due to the impermeable nature of all layers of the integument, and I find the same to be true of the hard seed of *Axyris amaranthoides*. It is generally assumed that in the Leguminosae the impermeability to water is never due to oily deposits. I find that the seed of the mesquite (*Prosopis juliflora*) is an exception. By soaking these seeds in ether for several days and then allowing the ether to evaporate, a large percentage is caused to germinate when germinative conditions are supplied, while a direct supply of germinative conditions brings only 5 to 10 per cent. The evaporation of the ether in which they have been steeped always shows an oily residue. Absolute alcohol is less effective in this case.

EWART says: "The seeds of the hawthorn are supposed not to germinate until after a year in the ground. CROCKER obtained no definite confirmation or negation of this fact, but here also it appears to be a case of the slow disintegration of the seed coats." This is hardly consistent with the statement (p. 284) in my paper on the rôle of seed coats.[4] In this case, however, I have underestimated the significance of the coats. I find that in *Crataegus mollis* embryos taken from apples just ripe and entirely freed from the two coats and endosperm begin growth within a few days after being

[1] EWART, A. L., On the longevity of seeds. Reprint Proc. Roy. Soc. Victoria N. S. **21**. pp. 210. 1908.

[2] BERGTHEIL, C., and DAY, D. L., On cause of "hardness" in seeds of *Indigofera arrecta*. Annals of Botany **21**:57–60. 1907.

[3] NOBBE, F., Handbuch der Samenkunde 117. 1876.

[4] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZETTE **42**:265–291. 1906.

put into the germinator, whether in light or dark. The removal of the inner coat and endosperm is done after sterilization, and the whole process, including germination, is conducted under aseptic conditions. One finds this a very tedious task and the resulting germination is of a peculiar type. In the light the cotyledons begin to expand and turn green. A small percentage of the roots begin growth within a week, but in a larger percentage the roots begin growth only after several weeks and after the cotyledons have expanded to several times their original size. Many of the radicles do not grow even after two months in the germinator. In the dark the growth is similar except that the cotyledons turn yellow and the radicles are even more tardy in their development. The coats then seem to play an important part in the delay, but the tardiness of the radicle in its development is of especial interest and reminds one of the behavior of the fungus-free orchid seeds,[5] or the upper seeds of the cocklebur with coats intact and in 76^{cm} of oxygen pressure.[4] A full investigation of the physiology of the germination of these seeds is now in progress by Mr. W. E. DAVIS and myself.

EWART again says: "CROCKER has, however, overlooked the fact that both the early and late seeds of *Xanthium echinatum* will germinate at 20 to 25° C. if the temperature is maintained for fourteen to twenty-one or more days instead of for eight to nine days." I assume that EWART means with coats intact, for that is the connection in which I have made my statement. On November 5, 1908, burs of this species were collected from the plants, the seeds removed from the burs, and the upper seeds soaked 18 hours, so as to show up any defective coats. Upper seeds with perfect coats were placed between wet filters in baths; one maintained at 24–25°, and one at 27–28°. On December 5 none had germinated. Of course with coats removed these seeds germinate within three days, even at 23°. In collections of this species from the crop of 1906 a small percentage of the upper seed with coats intact germinated at 30°. In collections of the crop of 1905, on which the work for my paper was done, the minimum temperature for the germination of these upper seeds lay between 32° and 33° even when they were kept in the germinator for a month. EWART says nothing about the time of gathering, precautions against defective coats, or the percentage germinating at 20–25°. In the absence of all these related data his statement can mean little. In *X. canadense* high temperatures are far less effective in overcoming seed-coat effects, and here a temperature fluctuating between 25° and 41° is most effective. A temperature of 40–43° for a few hours is often more effective than a lower temperature for a

5 BERNARD, N., On the germination of orchids. Roy. Hort. Soc. Rep. 3rd Internat. Congress on Genetics 292–296. 1906.

much longer period, a fact that led to the discovery of the temperature effects. In the light of this fact, EWART'S statement, "If burs are heated at 40° C. for a day or two, 50° for a few hours during soaking, a variable percentage of the later seeds will germinate within ten days," is not at all new. My data have shown that the effectiveness of high temperatures in overcoming seed-coat effects varies greatly with different species. Further, my data indicate that there is in this respect a slight variation in different crops of the same species gathered from the same locality, and it appears, if EWART'S data have been obtained with proper attention to sources of error, that there is a decided variation in seeds gathered from different regions of the globe.

EWART'S assumption that the coats in the seeds of water plants secure this delay by excluding oxygen does not seem to be true for some of these species. I have mentioned evidence for this in the case of the water hyacinth.[6] One of our students, working with the effects of oxygen on germination, tells me that seeds of *Alisma Plantago* germinate rather readily in entire absence of oxygen, provided the coats are ruptured. In the case of the upper seeds of *X. canadense* she finds that about 3^{cm} of oxygen pressure (0.2 that of the ordinary atmosphere) with two weeks' exposure is necessary to produce germination, even when the coats are removed. These results still need to be thoroughly tested. TAKAHASHI[7] has shown that seeds of rice germinate in entire absence of oxygen. It is probable, therefore, that the coats of the seeds of water plants secure delay in germination mainly by limiting the water supply, as I have pointed out.[6]

Through a discussion of minor and less significant details, however, we must not lose sight of the main conclusion, which is being more firmly established as more data are accumulated,[8] that delayed germination in seeds is generally, though not always, related to seed-coat characters rather than to so-called dormancy of protoplasm. The coat may limit the oxygen supply, as in the cocklebur; it may exclude or merely limit the water supply, as in the seeds of legumes on the one hand and of Iris and other water plants on the other; or it is possible, though not proved, that in some cases it may exclude other chemical compounds necessary for germination.

I believe I am doing EWART no injustice when I say that it is impossible to tell from his paper in how far it is a contribution and in how far a

[6] CROCKER, WM., Germination of the seeds of water plants. BOT. GAZETTE **44**: 375–380. 1907.

[7] TAKAHASHI, T., Is germination possible in absence of air? Bull. Coll. Agr. Tokyo **6**:439–442. 1905.

[8] KLUGH, G. F., Some cases of delayed germination in seeds. Science N. S. **28**:816. 1908.

compilation. In this way credit due other investigators appears to belong to EWART, and no one has suffered more in this respect than the writer.—WILLIAM CROCKER, *The University of Chicago.*

RESPIRATION CALORIMETER

On p. 133 of the second edition of Professor W. F. GANONG's admirable *Laboratory course in plant physiology*, which has just appeared, and a copy of which has come into my hands through his courtesy, I am interested to find a Dewar flask figured as a respiration calorimeter. Before my recent paper was published (BOT. GAZETTE **46**:193–202. 1908), I wrote to Mr. GANONG, knowing that he was preparing a second edition of his book, asking him to put my calorimeter into it. He wrote that his book had already gone to press. When my paper appeared he wrote again, saying that he "had been using the Dewar bulbs as a respiration calorimeter some four years past. . . . . Of course the point about the prior use of the bulbs is of no consequence whatever, and I mention it now because of the coincidence in your asking me to mention their use in my book."

So far as priority of use is concerned, it lies obviously with Mr. GANONG. To acknowledge this, and to record another of the curious coincidences which after all are not altogether rare in the history of science, is the purpose of this note.—GEORGE J. PEIRCE, *Leland Stanford Junior University.*

CRATAEGUS IN COLORADO

The attention of the writer has been called by Mr. W. W. EGGLESTON to a misstatement in an article in this journal for November, 1908. On p. 382, line 4, I should have said that the species described resembles most *C. erythropoda*, of the forms known to the writer in northern Colorado.—FRANCIS RAMALEY, *Boulder, Colorado.*

CURRENT LITERATURE

BOOK REVIEWS

The vegetation of Chile

The eighth volume of ENGLER and DRUDE'S *Vegetation der Erde* is a monograph on the vegetation of Chile by Dr. KARL REICHE[1] of the National Museum at Santiago. This is the first volume of the series to deal with American vegetation. REICHE'S long first-hand acquaintance with the Chilean flora makes this contribution a masterpiece, and all the more since fourteen years of effort have been spent with this volume in mind. Chile is to botanists the best-known part of South America, partly by reason of its peculiar accessibility, and partly by reason of the large number of foreign botanists who have made Chile their home, for a time at least. Among those who have contributed largely in recent years, and thus made REICHE'S work more readily possible, are PHILIPPI, JOHOW, NEGER, and DUSÉN. Of particular importance is the work of R. A. PHILIPPI, who was active for over half a century, and who died in 1904 at the age of 96. A short account of botanical investigation in Chile forms the introduction to the work, and there is given a bibliography of Chilean botany comprising 550 titles, of which R. A. PHILIPPI and his son contributed nearly one hundred.

No country in the world presents distribution problems of greater interest than those of Chile, as may be suspected by reason of climatological variation. The vegetation ranges from that of the desert of Atacama in the north, perhaps the driest of all deserts, to the rain forests of the south, where there is a rainfall of 250^{cm} per annum. In northern or tropical Chile (18°–30°) there is the region of desert where there are no marked seasons, and where agriculture is confined to the oases and river banks. In central or subtropical Chile (30°–38°) there are sharply marked dry and wet seasons, and the vegetation varies from steppes northward to sclerophyll forests southward. In southern or temperate Chile (38°–55°) there is a sharp distinction between the very rainy coastal district, where seasonal changes are relatively slight, and the interior, where the climate is dry and where the winters are cold and the summers hot. This rainy coastal strip is characterized by evergreens (temperate rain forest), while there is a strip of deciduous forest (probably the only such forest of consequence in the southern hemisphere) in the drier and periodic climate to the east. It will be noticed that this distribution of forest departs from that given by SCHIMPER in that the deciduous forest lies east rather than south of the evergreens.

[1] ENGLER, A., UND DRUDE, O., Die Vegetation der Erde. VIII. REICHE, KARL, Grundzüge der Pflanzenverbreitung in Chile. pp. xiv+374. *maps 2. figs. 55. pls. 33.* Leipzig: Wilhelm Englemann. 1907. *M*30.

The second part of the volume presents a detailed account of the most important families of vascular plants and their representatives, the vegetation forms, the formations, and the "biology" of the representative plants. Among the more interesting of the forest trees are the beeches (Nothofagus), of which five species are deciduous and three evergreen, and the conifers (Araucaria and Fitzroya); the latter forms swamp forests, perhaps comparable to our tamarack swamps. These conifers and beeches sometimes form pure forests, but most of the Chilean forests contain many tree species. Other important formations are the bamboo (Chusquea) thickets, xerophytic acacia thickets, and steppes.

The most detailed portion of the volume is that presenting the floristic features of the Chilean vegetation from north to south, and the delimitation of floral provinces. Many endemic species and monotypic genera are found in the country. The final chapters consider the relations of the Chilean flora to other floras (notably those of California, New Zealand, and Argentine), the life-history of the Chilean flora, and the modifications due to human influence. From the developmental standpoint the flora is made up of (1) a tropical contingent, the oldest of all, dating from the Mesozoic; (2) the Andine contingent, a xerophytic element associated with the rise of the Cordilleras; (3) the Californian and Mexican contingent; (4) the Antarctic contingent, mostly in southern Chile, and related to the New Zealand flora; (5) the boreal contingent, perhaps the most interesting of all, there being genera and even species in southern Chile that are common with the far north; (6) ubiquists and littoral pantropists; and (7) adventives. Many admirable plates add much to this important volume.—H. C. COWLES.

The pendulation theory

Now and then a geologist attempts to account for Permian glaciation within the tropics by supposing that the poles have shifted their position during the course of geologic history. Such theories are usually dismissed because they introduce more difficulties than they dispel. A few years ago PAUL REIBISCH, an engineer, laid before the *Verein für Erdkunde* at Dresden such a theory, known as the pendulation theory. There is now presented by Professor SIMROTH[2] of Leipzig a detailed account of the theory, together with a new alignment of facts of distribution. The essence of the pendulation theory is that the earth swings slowly to and fro upon an axis whose poles are in Ecuador and Sumatra. These poles are supposed to remain fixed, but the axial extremities that we commonly call the north and south poles are such for but a moment, speaking geologically. It will be seen that Ecuador and Sumatra must have been in the equatorial realm from the beginning, while for points now on the equator but 90° distant from these fixed poles (i. e. in the French Congo region and in the Pacific Ocean north of Samoa), there may have been in times past any conditions between polar

[2] SIMROTH, HEINRICH, Die Pendulationstheorie. pp. xii+564. *maps 27*. Leipzig: Konrad Grethlein's Verlag.] 1907. *M*12.

and equatorial. According to this theory, past variations in climate in any given place have been due to pendulation.

Glacial periods, such as the Permian and Pleistocene, have been developed through a poleward swing of regions now temperate; while warm periods, such as the Cretaceous and Eocene, have been developed by means of a swing toward the equator. At the present time Europe and eastern North America are supposed to be swinging southward and getting warmer, while western North America is swinging northward. Pendulation causes constant redistribution in the oceanic waters, by reason of the earth's oblateness, thus accounting for the submergence of coast lines.

The major portion of the volume is devoted to the presentation of the facts of distribution in animals as related to the pendulation theory. It is claimed that the various groups are more or less symmetrically distributed with reference to the fixed poles, owing to the control exerted on migration by the swinging of the earth on its axis of pendulation. One chapter only is given to plants, and in this chapter chief attention is paid to the conifers and Campanulaceae. Three maps are presented, showing the distribution of the conifers. In these and other maps southern Europe figures largely as a center of origin of forms and a center of migration, and the attempt is made to show that migration has taken place symmetrically from that region.

The volume as a whole has a strangely medieval atmosphere. Students of geographic distribution in these days are so accustomed to look carefully for facts that they have largely ceased to care for hypothetical disquisitions such as that of SIMROTH. One feels that the author regards the pendulation theory as a panacea, and that he selects for consideration those facts of distribution which fit it best. Certainly the problems of migration are vastly more than the symmetrical movement of organisms from a center under the control of the direction of pendulation. And the idea of pendulation itself seems more like an iridescent fancy than a reality. Biologists may well wait until there is some astronomic or geologic basis for such a hypothesis before they attempt to readjust their facts to the new theory.—H. C. COWLES.

MINOR NOTICES

Purple bacteria.—A monograph on Rhodobacteria[3] is the natural outcome of the results of shorter studies on the subject which have been presented from time to time by MOLISCH. After a discussion, partly historical, of methods of culture, the author describes eleven new species recognized by him and gives a classification, based upon those of WINOGRADSKY and MIGULA, in which he divides the order Rhodobacteria, containing all known purple bacteria, into two families: those which do and those which do not show sulphur granules in the cell substance. Turning to the biochemical side of the study, MOLISCH examines the relation of

[3] MOLISCH, HANS, Die Purpurbacterien nach neuen Untersuchungen. pp. 95. *pls.* 4. Jena: G. Fischer. 1907.

these organisms to light, oxygen, and organic substances. With regard to light, the purple bacteria do not ordinarily show positive phototaxis, but are incited to motility which continues for some time after the light is removed. They are not able to obtain carbon from carbon dioxid in the presence of light. Some forms are even anaerobic, and, unlike most pigment bacteria, can produce pigment under this condition. As to the pigment itself, MOLISCH distinguishes two kinds: the red (*bacteriopurpurin*) and a green (*bacteriochlorin*). The latter is distinct from cholorophyll, which fact agrees with that of their inability to use CO_2. MOLISCH concludes that nutrition from organic substance is somewhat related to light and the presence of pigment as shown by the increased energy caused by light; and that thus these forms stand between the colorless bacteria and the green algae.—MARY HEFFERAN.

The typhoid-coli group of bacilli.—Numerous methods have been proposed for the ready separation and identification of the typhoid and the colon bacilli in water. Such special media as LÖFFLER'S malachite-green, MACCONKEY'S lactose-bile, ENDO'S lactose-fuchsin, and CONRADI-DRIGALSKY'S crystal-violet, have been more or less successful in the hands of various workers. These are based upon substances which restrain the growth of one type of organism while allowing a characteristic development of the other. DUCAMP[4] proposes for this purpose the use of an "antibacilliary" broth prepared by cultivating in a lactose-peptone solution several strains of *B. coli*, for example, derived from different sources. This broth, when finally filtered germ-free, will be exhausted as a medium for *B. coli*, but will still allow the growth of *B. typhosus*. For the rapid detection of the latter in water, the sample is first plated in phenol broth and inoculations made from the colonies into lactose broth. If a race thus obtained grows in the anticoli and not in the antityphoid broth, and is agglutinated 1:50 by typhoid serum, it is undoubtedly *B. typhosus*.

Studies on the fermentative activities of the typhoid-coli-dysentery group resulted in the confirmation of some facts already known, and brought out some new affinities. *B. para-typhosus*, *B. enteritidis*, *B. psittacosis* Danysz and Thomassen, and hog cholera ferment the same sugars except for two races of hog cholera, which are inactive on xylose, dulcite, and mannose. *B. para-typhosus* Kurth in addition ferments saccharose and raffinose. *B. para-typhosus* A differs with respect to xylose, mannose, and dulcite.—MARY HEFFERAN.

NOTES FOR STUDENTS

Subterranean fungi.—ED. FISCHER has recently made a contribution[5] to the morphology of the fungi. The paper is based on the study of material collected

[4] DUCAMP, LOUIS, Contribution à l'étude de la différentiation du colibacille et du bacille typhique. Action des bacilles du groupe coli-typho-dyssentérique sur les hydrates de carbone. pp. 181. *pl. 1.* Thesis. Lille. 1907.

[5] FISCHER, ED., Zur Morphologie der Hypogaeen. Bot. Zeit. **66**:141–168. *pl. 6.* 1908.

by Dr. W. A. SETCHELL and Dr. N. L. GARDNER in the region of Berkeley, California, during the years 1903–1905. It is of especial interest and importance in view of the fact that so little attention has been given heretofore to the collection of subterranean fungi in North America, and because this new material, some of it in young stages, has enabled the author to put some of the imperfectly described genera of HARKNESS on a better footing, and to revise some of his own opinions as to the systematic position of certain genera which have occupied an unsatisfactory position.

Some of the more important results are as follows: *Myrmecocystis cerebriformis* Harkness and *M. candida* Harkness are shown to be identical, the former being an older and mature stage, while the latter is unripe material of the same species. The former name has precedence. *Myrmecocystis* Harkness (1899) is also shown to be generically identical with *Pseudogenea vallisumbrosae* Bucholtz (1900), and the latter becomes *M. vallisumbrosae* (Bucholtz) E. Fischer. Young material of Piersonia, a genus imperfectly described by HARKNESS from old material, shows that this is a very interesting genus. The small nests of asci in the interior of the fruit body are arranged in separate, pouchlike segments of hymenia, with the free ends of the asci facing open passages or chambers terminating the *venae externae*, the point of junction being rather abruptly narrowed. Paraphyses are irregularly distributed among the asci in groups or partly wanting, but line the surface of the *venae externae*. The latter in the deeper parts of the fruit body are filled with a loose weft of hyaline hyphae developed from the ends of certain of the paraphyses; while toward the external portion of the fruit body brown hyphae are intermingled and become more abundant as the openings of the *venae externae* are reached. In the arrangement and form of the asci Piersonia resembles Pachyphloeus, the absence of hyphae in the hymenia-lined passages recalls Hydnotrya; but the most characteristic feature in which Piersonia differs from other genera is the sharply localized condition of the hymenial parts, since in all other Eutuberineae the *venae externae* are lined throughout by the hymenium. In this respect Piersonia represents a special type at one extreme of an arm in the series Eutuberineae, in which the ascus hymenium has disappeared from a large portion of the *venae externae* and is found only at the innermost terminations of the infolding of the same. FISCHER suggests that Piersonia may give the clue to the proper interpretation of the structure of Choiromyces which he has formerly placed with the Plectascineae, where it certainly occupies a rather anomalous position with its distinct hymenium. His suggestion now is that the large, irregular pouchlike hymenial portions in the fruit body of Choiromyces may, like the smaller ones of Piersonia, stand at the terminations of the *venae externae*, which in Choiromyces have become completely and evenly filled, and all evidence of their communication with the outside may have thus disappeared. FISCHER merely offers this as a suggestion. It will require developmental studies of young material to decide the point. Should this prove to be the true interpretation, it would lend some support to MATTIROLO's view that the difference between the Plectascales and Tuberales is not fundamentally sufficient to warrant their

separation into two groups, although FISCHER has contended, and still maintains, that there is no intermediate type between the two groups; since if his suggestion as to the interpretation of Choiromyces proves to be correct, this anomalous structure would indicate subsequent modification of the *venae externae* and not an ontogenetic connection with the Plectascineae.

Pseudohydnotrya, founded by FISCHER in 1896 on material from California, he now finds is not related to *Hydnotrya* Berk. and Broome, a member of the Eutuberineae, but is generically identical with *Geopora* Harkness, which is closely related to *Hydnocystis* Tul. The fruit body of Hydnocystis possesses a single large hollow space which opens to the outside, though the opening is filled with hairs. The wall of the hollow space is clothed with the hymenium. Geopora is a Hydnocystis in which the hymenial walls are deeply infolded in an irregular and complicated manner, in some species closed from the outside, in others communicating in some places with infoldings of the external walls. All recent students of this group agree in placing Hydnocystis among the Pezizaceae, and FISCHER locates Geopora here also, although he formerly placed these two genera among the Balsamiaceae, where they occupied an anomalous position.

One of the very interesting forms proved to be the type of a new genus, *Pseudobalsamia*, which resembles Balsamia in external appearance, but differs in the presence of *venae externae* which open to the outside, thus agreeing with the Eutuberineae. It also differs from Balsamia in the absence of distinct trama plates or veins (*venae internae*), or rather in the masking of them by the irregular distribution of the asci among the tissue elements. In this latter character it resembles the Plectascineae. The *venae externae*, however, are lined with paraphyses, and occasionally asci are found in this layer parallel with the paraphyses. Pseudobalsamia, then, is regarded as one of the Eutuberineae, in which by secondary modification the asci have withdrawn from their regular position in a hymenium and have become intermingled with the elements of the trama, thus simulating one of the characters of the Plectascineae, without showing any ontogenetic connection with that series. This leads FISCHER to regard Hydnobolites, formerly placed by him in the Plectascineae, as one of the Eutuberineae, since the hymenium has probably undergone a similar modification, and the *venae externae* open to the outside. This view of the relationship of these two genera is strengthened by the well-known fact that the asci are often distributed in the trama in certain species of Tuber, as in *T. brumale*, and *T. rufum;* while BUCHOLTZ has shown that in the development of *T. puberulum* the tissue corresponding to the trama areas (*venae internae*) become compressed and changed by the pressure of the developing asci.

The modification which FISCHER's views on the systematic arrangement of the ascomycetous Hypogeae have undergone as a result of this study are expressed in a résumé. Briefly this is as follows:

1. The *Plectascineae series*, with asci scattered in the tissue of the interior of the fruit body, or in groups, not forming hymenia, includes the two families Elaphomycetaceae and Terfeziaceae. In the latter family remain the genera

Eoterfezia (as a simple form), Terfezia, Tirmania, Terfeziopsis, Picoa (incl. Phaeangium), Delastria, Delastreopsis (as higher differentiated forms). Genabea, Choiromyces, and perhaps also Hydnobolites and Pseudobalsamia are excluded from the Plectascineae, and probably go to the Eutuberineae series.

2. The *Balsamiaceae*, with asci in definite hymenia lining the walls of chambers closed to the outside, includes the single genus Balsamia. Hydnocystis and Geopora go to the Pezizaceae. (See ED. FISCHER, Hedw. **30**:56–60. 1898.)

3. The *Eutuberineae series*, with hymenia lining the walls of interior passages which open to the outside and are either hollow or more or less filled with hyphal wefts (asci rarely withdrawn from hymenia into the trama), includes the gymnocarpic forms and are probably derived from the simpler Helvellales like Rhizina and Sphaerosoma.

Since the second series is represented by the single genus Balsamia, with a hymenium lining interior passages of the fruit body, one is led to inquire if it would not be a more satisfactory arrangement to recognize two series: (1) the Plectascales as outlined above, and (2) the Tuberales, including the Eutuberineae and Balsamia. May it not be possible that Balsamia has been derived from some of the Eutuberineae by a secondary modification of such a nature that the interior passages have become closed from the outside; just as in Geopora, as FISCHER points out, examples occur in which such a secondary modification has probably taken place? The development of Balsamia should be studied with this in view.

Among the basidiomycetous Hypogeae several collections of Hysterangium furnish additional evidence of the existence of a *Hysterangium-Clathraceae series* beginning with Gautieria, and then passing from Hysterangium through Phallogaster, Protubera, etc., to the Clathraceae.

The paper abounds in speculative discussion as to relationship and ontogeny, which is a characteristic of FISCHER'S contributions. In a number of instances his views seem to be based on rather insufficient evidence, which is perhaps the chief adverse criticism which may be made on this contribution. Some of them appear to be well founded, and certainly his present views on the classification of the ascomycetous Hypogeae are to me much more satisfactory than his arrangement in ENGLER & PRANTL'S *Pflanzenfamilien*. It should be said, however, that all his suggestions and speculations are stimulating to thought, and I trust will also stimulate collectors and investigators to bring to the light the riches in subterranean fungi which are awaiting us in this large field of North America.—GEO. F. ATKINSON.

Cytological basis of Mendelism.—GRÉGOIRE[6] has published a critical discussion of current cytological theories, with particular reference to their bearing on the interpretation of Mendelian phenomena. Certain fundamental hypotheses

[6] GRÉGOIRE, V., Les fondements cytologiques des théories courantes sur l'hérédité Mendélienne. Ann. Soc. Roy. Zool. et Malacol. Belgique **42**:267–320. *figs. 4.* 1907.

will be mentioned first. His view of the individuality of the chromosomes is based quite largely on his well-known observations, and those of his pupils, on the resting stage of the nucleus compared with the late telophase and early anaphases of mitosis. The attempts of FICK,[7] TELLYESNICZKY,[8] and others to disprove individuality, come in for pointed criticism. GRÉGOIRE concludes that "Il est certain que les chromosomes persistent dans leur individualité, sous la forme de continus structuraux, à travers toute l'ontogénèse." Regarding reduction, he considers it certain that the heterotypic mitosis dissociates the n chromosomes, received by the reproductive mother cells, into two groups of $n/2$; and probable that a paternal chromosome always conjugates with a maternal of the same form. But he finds nothing to *prove* that a pair of allelomorphic characters is fixed only in one pair of chromosomes, nor that the chromosomes conjugated in the heterotypic gemini are homologous maternal and paternal chromosomes.

The hypotheses necessary to explain Mendelism on a cytological basis are given as follows: (1) The chromosomes play a preponderant rôle in the transmission and determination of hereditary characters. (2) The different chromosomes of a given cell are bearers of different properties. (3) In the chromosomes of a hybrid egg a Mendelizing character is represented only by two chromosomes, one maternal, one paternal. In one of these the character is represented in a recessive condition (modalité recessive), in the other in the dominant condition.

It must be said (and GRÉGOIRE would probably agree with this) that the conception of representative particles in the dominant and recessive condition merely projects the phenomena of dominance back into the germ cell without attempting an analysis of its meaning, or how it comes about, and hence explains nothing. This appears to the reviewer to be a serious and probably fatal objection to the last hypothesis.

On the basis of these hypotheses the germ cells would receive of each pair a single recessive chromosome (maternal or paternal) and a single dominant chromosome (maternal or paternal). In the prophase of the heterotypic mitosis the chromosomes join in pairs, and observation favors the view that these are homologous maternal and paternal chromosomes. Then after reduction half the germ cells would receive a "dominant" chromosome, and half the corresponding "recessive" chromosome. We thus arrive at MENDEL'S conception, and the chances of meeting he described between germ cells are here conceived between chromosomes. Granting the three hypotheses then, Mendelian phenomena would be expected to result.

In Pisum eleven or more pairs of allelomorphs have been observed and the reduced number of chromosomes is only seven; which shows that in this case, at

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[7] FICK, Betrachtungen über die Chromosomen, ihr Individualität, Reduktion und Vererbung. His-Waldeyer's Archiv. 1906; Vererbungsfragen, Reduktions- und Chromosomenhypothesen, Bastard-Regeln. Engeb. Anat. Ent. 1907.

[8] TELLYESNICZKY, Zur Kritik der Kernstrukturen. Archiv. Mikr. Anat. **60**: 681–706. 1902; Ruhekern und Mitose. *Idem* **66**: 367–433. 1905.

least, several characters must reside in one chromosome. The characters must then be confined to separate particles or corpuscles of the chromosomes, and an interchange of homologous particles according to chance during maturation would give the Mendelian combinations. Many observers, including STRASBURGER, ROSENBERG, ALLEN, and SCHREINER, have described such an interchange of particles; but GRÉGOIRE's conclusion, which he has emphasized before, is that nothing in the observations of the nuclear reticulum, the somatic spirem, or the heterotypic spirem justifies the admission of representative particles, chromatic or achromatic. The "chromomeres" observed particularly in the heterotypic spirem, he considers not as autonomous granules imbedded in a substratum, but merely as a substratum impregnated with chromatic material and rather regularly alveolated, giving the appearance of a single or double row of "chromomeres."

GRÉGOIRE further denies that there is an interchange of particles between the parallel filaments in the double spirem stage, such as various cytologists have described. These two facts, namely, the presence of autonomous particles and their free interchange at some time during the reduction processes, would appear to be essential to a cytological basis for Mendelian phenomena.—R. R. GATES.

Extra-floral nectaries and "myrmecophily."—To many who have held the untenable view that plant structures are necessarily useful, extra-floral nectaries have been a stumbling-block. NIEUWENHUIS-UEXKÜLL[9] has made an exhaustive study of the extra-floral nectaries of 100 species of plants growing at Buitenzorg, and it may be said that these studies are of great importance because they show conclusively that we know nothing concerning the advantage of these peculiar organs. There is an admirable critical review of the treatises that consider extra-floral nectaries, beginning with HALL's study in 1762. The term extra-floral nectary was first employed by CASPARY in 1848, who rather inclined toward LIEBIG's theory that they are of value to plants as a means of excreting sugar when present in excess. The classic study of these organs is DELPINO's treatise issued in 1874, in which the term extra-nuptial nectaries is employed, and the idea advanced that the sugar they secrete attracts ants; these insects in turn are supposed to defend such plants against their enemies. Simultaneously with DELPINO, BELT proposed a similar theory for *Acacia sphaerocephala*, and from then until very recently botanists have generally believed in the existence of myrmecophiles, or ant-loving plants. Among the supporters of myrmecophily have been DARWIN, FRITZ MÜLLER, TRELEASE, and SCHIMPER. BONNIER (1878) regarded all nectaries as sugar reservoirs, any other function being thought quite incidental, and KERNER (1878) regarded extra-floral nectaries as protective against "unbidden guests." Beginning with the skeptical attitude taken toward myrmecophily by VON IHERING in 1894, there have been critical contributions by

[9] NIEUWENHUIS VON UEXKÜLL-GÜLDENBANDT, M., Extraflorale Zuckerausscheidungen und Ameisenschutz. Ann. Jard. Bot. Buit. II. **6**:195–327. 1907.

RETTIG, ULE,[10] and others, all of which are out of harmony with the myrmecophile hypothesis. The work of NIEUWENHUIS-UEXKÜLL confirms these more recent views.

After a detailed account of extra-floral nectaries by plant families, the author summarizes the data presented, and some of the chief conclusions follow. The structure and form of the nectaries do not favor the theory that they originated as adaptations for ant protection; in many cases they specifically oppose such an assumption, and their position on the plant (largely on the leaf undersurface) is such as to be of no purposive significance. The secretions often begin late in life, so that the plant is without protection in youth, when it is most needed. In other cases the secretion begins in early youth and soon ceases, thus leaving the plant for a long time without ant protection, if such exists. The nectaries usually secrete sugar somewhat spasmodically during their period of activity, and are often dry. The nectar of many species is avoided by ants and other animals. The view that the honey-seeking ants drive off crawling insects and other "unbidden guests" that mutilate the flowers, robbing them of honey or pollen, is quite untenable, there being no relation between mutilated flowers, ants, and extra-floral nectaries. Floral mutilation depends on the structure and position of the flower or the weather; furthermore, most mutilated flowers produce as many seeds as flowers that are not mutilated. The honey-seeking ants are not combative and do not attack other insects on the plants they visit; indeed, these other insects often attack and repel the ants. The nectaries, therefore, so far from being beneficial structures developed by natural selection, are harmful to the plants of which they are a part, in that they attract insects of all kinds, which not only eat the sugar but do harm in various ways. Observation showed that individual plants which secreted little or no nectar are less harmed by insects than are those that produce nectar.

This paper, in addition to other recent work, makes it clear that myrmecophily is a figment of the imagination, and the word should be dropped from botanical literature. Ants may "love" plants, but there is no evidence that plants "love" ants. Plants inhabited by these insects, if it seems worth while to group them, may be called myrmecophytes.—H. C. COWLES.

A Mendelian ratio and latency.—SHULL[11] in a suggestive paper makes further contributions to Mendelian theory. In certain bean hybrids three distinct units were shown in earlier papers[12] to be involved, namely, a pigment factor, a blackener, and a mottled pattern. In the last character a peculiar condition is found, namely, the mottled pattern depends upon the presence of a mottling allelo-

[10] See BOT. GAZETTE **44**:314. 1907.

[11] SHULL, GEO. H., A new Mendelian ratio and several types of latency. Amer. Nat. **42**:433–451. 1908.

[12] ———, The significance of latent characters. Science **25**:792. 1907; Some latent characters of a white bean. *Idem* **25**:828. 1907.

morph in a *heterozygous* condition, the homozygous giving unmottled seeds. This peculiarity results in a new ratio, 18:18:6:6:16, instead of the anticipated 27:9:9:3:16. Latency is held to mean invisibility and not inactivity or dormancy. BATESON'S "presence and absence" hypothesis, in which the presence of any character is said to be dominant to its absence, is believed to be of general validity; and his[13] more recent terms "epistatic" and "hypostatic," as applied to the capacity of one unit to hide or be hidden by another, are accepted. Thus in MENDEL'S original case, yellow in cotyledons is not to be considered "dominant" over green, but dominant to the absence of yellow and "epistatic" to green, i. e., according to SHULL, causing its "invisibility" but not its "inactivity." This change of view involves some nice distinctions, but appears to obviate some of the difficulties of the older view of dominance, especially in connection with ontogeny. Incidentally all that remains of the Mendelism of MENDEL is his hypothesis of gametic purity. The superstructure erected upon this has grown in complexity with great rapidity.

With latency thus clearly defined, four types of latency are discussed: (1) "*Latency due to separation*, in which an allelomorph when acting alone has no external manifestation, and is only rendered patent by combining it with another allelomorph." This type of latency is not uncommon, and gives rise to such ratios as 9:3:4, 9:7, 27:9:28. (2) "*Latency due to combination*, in which two dominant allelomorphs, each giving rise to a peculiar character when acting alone, lose their external manifestation when coexisting in the same zygote." This gives the ratio first mentioned above in mottled beans, and may account for certain "mid-races." (3) "*Latency due to hypostasis*, in which the presence of one allelomorph cannot be detected owing to the presence of another allelomorph, the character produced by the latter being unmodified by the activity of the former." For example, a black bean is shown to hide a distinct-brown allelomorph, and a dark orange bean to carry invisibly a light-yellow allelomorph. This condition may give such a ratio as 12:3:1. (4) *Latency due to fluctuation*. Disappearance of characters under unfavorable conditions of nutrition, etc.; a very common phenomenon which may cause discrepancies from the expected ratio. Some of the cases formerly called "incomplete or partial dominance" would probably be classed here. Ratios may also rarely be modified by the failure of certain allelomorphic combinations to form a zygote which will develop.—R. R. GATES.

Respiratory chromogens.—PALLADIN[14] has devised a new, very simple, and effective method of detecting the respiratory chromogens in plants. He uses this method to show the wide distribution of these chromogens in the plant kingdom. In 71 species, ranging from liverworts to dicotyledons, this method showed these

[13] BATESON, WILLIAM, Facts limiting the theory of heredity. Science **26**:649–660. 1907.

[14] PALLADIN, W., Die Verbreitung der Atmungschromogene bei den Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**:378–389. 1908.

chromogens in 67. Their existence in three of the other four species can be demonstrated by other methods. He mentions various fungi that other investigators have shown to contain chromogens, as well as various other higher forms. The points in the literature of this very important subject are briefly and clearly stated.

The same investigator finds[15] that portions of leaves in a 20 to 25 per cent. saccharose solution for seven days show a great increase in respiratory chromogens, over checks immediately taken from the plant, or those kept in distilled water for the same length of time. Illumination during the treatment increases somewhat the chromogen production. If this treatment is continued for 17 days in light, the portions of leaves take on a bright-red color. The color he believes originates from the oxidation of respiratory chromogens. He holds that the sugar greatly increases the respiration and therefore the respiratory chromogens. Whether the chromogen shall become chromatic depends upon whether the oxidases exceed the reductases in activity. In long-continued exposures this seems to occur, hence the red color. He believes that OVERTON's explanation of spring and autumn coloration of leaves is not complete with the consideration of low temperature (as lowering respiration) and abundant supply of sugar as the factors, and considers the relative activity of oxidases and reductases on the chromogen products of respiration as very important.—WILLIAM CROCKER.

Graft hybrids.—WINKLER[16] has begun a series of experiments in the endeavor to produce graft hybrids, such as the well-known *Cytisus Adami* is believed to be. He uses for this purpose certain members of the Solanaceae and Capparidaceae. The method is to graft one species on another in the ordinary manner, and after the scion has "taken," to sever the stem at a point where the tissues of both species will be cut. Adventive shoots then grow out from this cut surface. These will have the characters of either species according to the point they grow from. Shoots arising from the point of contact of the two species gave a peculiar result, which may be described. A scion of *Solanum nigrum* was grafted in this way on a seedling of *S. lycopersicum*, and the shoot in question, originating from the point of contact of the parental tissues, bore leaves having on one side of the stem the characters of *S. nigrum*, and on the other side those of *S. lycopersicum*. In certain cases where leaves were situated on the meeting-line of two kinds of cells, one-half of a leaf showed the characters of either parent. WINKLER proposes to call such organisms, in which one side resembles either parent, "chimeras," and for this plant proposes the name *Chimera Solanum nigrolycopersicum*. He concludes that the cells of two different species may come together in other than a sexual way, and thus serve as the starting-point for an organism which shows simultaneously the characters of both parent species.—R. R. GATES.

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[15] PALLADIN, W., Ueber die Bildung der Atmungschromogene in den Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**: 389–394. 1908.

[16] WINKLER, HANS, Ueber Propfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesells. **25**: 568–576. *figs.* 3. 1907.